TESTING DARWIN'S NATURALIZATION CONUNDRUM BASED ON TAXONOMIC, PHYLOGENETIC AND FUNCTIONAL DIMENSIONS OF VASCULAR PLANTS

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Running Header: Dissecting Darwin's naturalization

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Abstract

Charles Darwin posited two alternative hypotheses to explain the success of nonnative species based on their relatedness to natives: non-native species that are closely related to native species could experience i) higher invasion success because of an increased probability of habitat suitability (conferred by trait similarity), or (ii) lower invasion success due to biotic interference, such as competition and limiting similarity. The paradox raised by the opposing predictions of these two hypotheses has been termed 'Darwin's naturalization conundrum' (DNC). Using plant communities measured repeatedly across an experimental fire gradient in an oak savanna (Minnesota, USA) over 31 years, we evaluated the DNC by incorporating taxonomic, functional and phylogenetic information. We used a 'focal-species' approach, in which the taxonomic, functional, and phylogenetic structure of species co-occurring with a given nonnative (focal) species in local communities was quantified. We found three main results: first, nonnative species tended to co-occur most with closely related natives, except at the extreme ends of the fire gradient (i.e., in communities with no fire and those subjected to high fire frequencies); second, with increasing fire frequency, nonnative species were functionally more similar to native species in recipient communities; third, functional similarity between co-occurring nonnatives and natives was stable over time, but their phylogenetic similarity was not, suggesting that dynamic external forces (e.g., climate variability) influenced the phylogenetic relatedness of nonnatives to natives. Our results provide insights for understanding invasion dynamics across environmental gradients and highlight the importance of evaluating different dimensions of biodiversity in order to draw stronger inferences regarding species co-occurrence at different spatial and temporal scales.

Introduction

The assembly and maintenance of ecological communities is a dynamic process operating over multiple spatial and temporal scales,

including niche-based interactions and sorting at local spatial scales to stochastic and historical processes at large spatial scales (Leibold et al. 2004, Tilman 2004, Cavender-Bares et al. 2009, 2018a, Pinto-Ledezma et al. 2019). Over the past millennium, human activities have greatly influenced these processes through mechanisms like habitat degradation and span style="font-family:'Times New Roman'">movement of species outside of their native ranges, with negative consequences for biodiversity, ecosystem functioning, and human well-being (Sax et al., 2007, Thuiller et al. 2010, Vilà et al. 2011, Simberloff et al. 2013, Capinha et al. 2015). In this paper, we address some of the processes important to invasion by nonnatives at local scales, using a novel, 31-year data set from an oak savanna ecosystem in which different units were experimentally subjected to different fire regimes.

Biological invasions are a major driver of community change (Pearson et al. 2018), especially in the Anthropocene (Capinha et al. 2015). Understanding the causes of invasion success has become a major goal in ecology, evolution, and conservation (Dawson et al. 2017). Among myriad hypotheses proposed to explain the outcomes of nonnative species invasion (Catford et al. 2009, Jeschke 2014, Enders at al. 2020), two key hypotheses incorporate evolutionary relatedness as a primary consideration (Gallien and Carboni 2017, Ma et al. 2016, Cadotte et al. 2018). Darwin's naturalization hypothesis (DNH; Fig. 1A) suggests that nonnative species that are closely related to resident native species are less likely to invade native assemblages because their niches are effectively occupied by ecologically similar species already (Daehler 2001). In contrast, the pre-adaptation hypothesis (PAH; Fig. 1B) postulates that nonnative species closely related to resident natives should be favored precisely because of their niche similarity with native species, i.e., they are likely to possess traits that make them well-suited to the new habitat (Ricciardi and Mottiar 2006). Both of these hypotheses effectively use phylogenetic relatedness as a surrogate for functional similarity, with functional similarity inhibiting invasion via limiting similarity and competition or facilitating invasion via habitat suitability and pre-adaptation. Accordingly, the extent to which nonnative species are closely or distantly related to resident natives may inform whether competitive interactions or environmental filters and sorting processes, respectively, are dominant factors determining invasion success (Gallien and Carboni 2017, Cadotte et al. 2018). These opposing hypotheses both trace back to Darwin (1859) and together comprise the so-called 'Darwin's naturalization conundrum' (DNC, Diez et al. 2008, Thuiller et al. 2010, Cadotte et al. 2018).

Several studies have evaluated the DNC across different spatial scales and systems (for a review see Ma et al. 2016, Gallien and Carboni 2017, Cadotte et al. 2018). However, few studies—with mixed results—have explored the dynamics of species composition and relatedness within communities during the invasion process (Blackburn et al. 2015, Li et al. 2015). Indeed, nonnative species are continually expanding or retracting their ranges in the regions they have colonized (Sax et al. 2007, Blackburn et al. 2015, Pannell 2015), potentially as a result of fluctuating availability of resources and disturbance regimes in the invaded communities (Lonsdale 1999, Davis et al. 2000, Shea and Chesson 2002, Shea et al. 2004, Pearson et al. 2018). Thus, the presence of nonnative species in a community does not necessarily indicate that they are well-adapted to the new environmental or niche conditions. Indeed, the evolution of nonnatives under different environmental conditions may make them poorly adapted to the new environment (Shea and Chesson 2002, Catford et al. 2012) and they may not have positive population growth rates within patches of their invaded range (Chesson 2000, Davis et al. 2000, Shea and Chesson 2002, Shea et al. 2004, Pearson et al. 2018).

Although there has been considerable research into traits associated with species invasiveness (van Kleunen et al. 2010), relatively few studies have explicitly considered the role of functional traits in mediating colonization, establishment (Carboni et al. 2018, Catford et al. 2019, 2020) and long-term persistence (Marx et al. 2015, Catford et al. 2019) of nonnative species in local communities. Although several recent studies have generally found similar results—from a phylogenetic perspective, nonnative species tend to coexist more with their close relatives (e.g., Li et al. 2015, Marx et al. 2015, Williams et al. 2018, Kusumoto et al. 2019)—the incorporation of functional information into analyses provides new insights regarding functional differentiation between

coexisting natives and nonnative species (Cavender-Bares et al. 2009, Cadotte et al. 2018).

In this study, using plant communities sampled over three decades across an experimental fire gradient at Cedar Creek Ecosystem Science Reserve (hereafter Cedar Creek) in Minnesota, USA, we evaluate Darwin's naturalization conundrum (DNC) by explicitly incorporating taxonomic, functional, and phylogenetic information into our analyses. We apply a novel approach based upon the framework of Villalobos et al. (2013, 2017, see aso Barnagaud et al. 2014), extending the concept of species' '*phylogenetic/functional fields*'—the overall phylogenetic/functional structure within a given species' geographical range (Villalobos et al. 2013)—to describe the phylogenetic/functional structure of species that co-occur with a focal species within particular local communities (hereafter, 'focal-species approach'; Box 1). Note that our focal-species approach differs from the original "species field" concept in that it measures the phylogenetic/functional structure of those species that co-occur with a focal species in a particular community (which can be defined at different spatial scales, depending on the question and context), instead of doing so across species found within the full geographical range of the focal species. In doing so, this approach addresses co-occurrence of different sets of species within separate communities rather than a single set of species across a geographical range (Box 1). Specifically, each species within a community is in turn selected as a focal species, its phylogenetic/functional distance to each of the other species within the community is calculated, and the resulting values per focal species are averaged (e.g., mean pairwise distance per focal species, MPD_{focal}; Fig. 1A-B). By focusing at the level of local communities, the focal-species approach enables measuing whether a nonnative species occurs more frequently with phylogenetically close/functionally similar or phylogenetically distant/functionally dissimilar species. It can thus be used to make inferences regarding processes (e.g., niche-based interactions, environmental sorting, stochastic processes) shaping local patterns of community assembly and species co-occurrence (Leibold et al. 2004, Cavender-Bares et al. 2009).

Predictions for Darwin's naturalization conundrum along Cedar Creek's fire frequency gradient

Based on previous studies that evaluated DNC (e.g., Diez et al. 2008, Davies et al. 2011, Carboni et al. 2013, Bezeng et al. 2015, Marx et al. 2016), we expected that nonnative species would tend to co-occur more with 1) distantly related species (phylogenetic overdispersion, DNH), or 2) closely related species (phylogenetic clustering, PAH) (Fig. 1C). The same logic extends to the influence of functional traits on species co-occurrence (Fig. 1C): if co-occurring nonnative and native species are functionally similar, this would support the hypothesis that environmental fit mediates specis co-occurrence within invaded communities; conversely, if co-occurring species are functionally distinct, this would support the premise that competition governs co-occurrence between native and nonnative species (Gallien et al. 2014, Carboni et al. 2018, Cadotte et al. 2018).

The experimental fire frequency gradient at Cedar Creek provides a unique opportunity to test DNC and explore temporal changes in focal-species relatedness across both phylogenetic and functional dimensions (Fig. 1A-B). Specifically, as local conditions become more and differentially stressful (e.g., repeated fires versus deep shade at the two ends of the fire-frequency gradient; Peterson and Reich 2001, Willis et al. 2010, Cavender-Bares and Reich 2012), populations of individual species are expected to increase or decrease as a function of environmental sorting on their traits (Leibold et al. 2004, Mayfield and Levine 2010, HilleRisLambers et al. 2012). Consequently, only species that have evolved to tolerate fire exposure and dry, high-light conditions on the frequently burned end of the gradient, or to compete for light on the shady, unburned end of the gradient, are able to recruit and persist over time. Functional traits related to dispersal, establishment, persistence, resource acquisition, and recovery after disturbance (e.g., specific leaf area [SLA], plant height, seed mass and rooting depth; Moles et al. 2005, Peterson and Reich 2008, Willis et al. 2010, Cavender-Bares and Reich 2012, Díaz et al. 2015, Pinto-Ledezma et al. 2018) will likely affect species' responses

to fire regimes. See Box 2 for a description of the expected changes in species' functional traits along Cedar Creek's fire frequency gradient.

Considering species' evolutionary and ecological differences, and given that traits and phylogeny are linked due to underlying trait evolution (Fig. 1C), we test multiple predictions for explaining variation in focal nonnative species phylogenetic relatedness/functional similarity across environmental gradients (Fig. 2). We posit that frequent fire—which is accompanied by nutrient depletion in this system—is more stressful than deep shade and heavy competition for light. Moreover, we hypothesize that there is antagonism between environmental stress and competitive interactions between the invader and its closely related native species, such that the likelihood of competitive exclusion weakens as environmental stress becomes greater. An alternative hypothesis would be that deep shade and strong light competition are equally stressful, but in ways that differ from frequent fire. Testing our hypotheses, as articulated below, will illuminate these scenarios and how relate to invasion and the DNC.

Prediction 1: For species' functional traits that are conserved over evolutionary time (Fig. 1C), we predicted that relatedness of focal nonnative species to native resident species would shift from a pattern of phylogenetic overdispersion (low phylogenetic relatedness) to phylogenetic clustering (high phylogenetic relatedness) with increasing fire frequency (Fig. 2A). That is, we expected that closely related and functionally similar plants—specifically those with low SLA, deep roots and short height—would co-occur more in communities subjected to high fire frequency. We further expected these same plants to be excluded from low fire-frequency regimes that, instead, would be dominated by functionally distinct and distantly related taller species that can persist under conditions of low understory light and soil fertility (e.g., shade-tolerant woody and herbaceous species; Cavender-Bares et al. 2004, Peterson and Reich 2008, Willis et al. 2010).

Prediction 2: Conversely, for functional traits that are evolutionary convergent (Fig. 1C), shifts from phylogenetic clustering to phylogenetic overdispersion are predicted with increasng fire frequency (Fig. 2B). That is, we might expect nonnatives to co-occur more with distantly related but functionally similar natives with increasing fire frequency (Fig. 1C). Note that these predictions are based on phylogenetic distances between focal nonnatives and co-occurring species within recipient communities (Box 1). Under this prediction, the steeper the environmental gradient (e.g., a gradient from unburned to high fire frequency; Fig. 2B), the more nonnative species should be able to avoid competition with ecologically similar native species (C_4 grasses versus forbs; Leach and Givnish 1999). As a consequence, nonnative species are not excluded from native communities subjected to high fire frequency, where environmental filtering and sorting processes dominate due to the sunny, hot, dry, and nutrient−poor conditions where these communities are distributed (White 1983, Leach and Givnish 1999, MacArthur and Levins 1967, Peterson and Reich 2008, Cavender-Bares et al. 2009).

Prediction 3. Ultimately, these dynamics may be quite complex. If biotic and abiotic filtering and sorting are acting simultaneously (Ackerly 2003, 2004, Swenson and Enquist 2009, Germain et al. 2018), and functional traits show phylogenetic signal, traits of the focal nonnative species should tend to be either similar to (clustered) or distinct from (overdispersed) native species in the community (Fig. 1C). This would result in a complex nonlinear trend of changes in focal nonnative species' relatedness across the fire frequency gradient. For instance, as environmental conditions shift from communities with no fire to communities frequently subjected to fire (Fig. 2C), nonnative species would tend to co-occur mostly with closely related species, given that disturbances, such as fire regimes, filter or eliminate disturbance-sensitive species (Huston 1979). Thus, different fire regimes can select for fire-resistant species (e.g., graminoids and forbs) over shade-tolerant and fire-sensitive species (e.g., woody plants) (Peterson and Reich 2001, 2008). Once functionally similar species capable of tolerating conditions of frequent fire co-occur (e.g., graminoids and forbs), biotic forces may become more important such that nonnative species may tend to co-occur with

distantly related but ecologically similar species (e.g., light-demanding and fire-resistant) (Fig. 1C).

Methods

Study site

The study was conducted within a large-scale 50-year fire frequency experiment at Cedar Creek. Cedar Creek is a 2300-ha reserve and National Science Foundation (NSF) Long Term Ecological Research site located on the Anoka Sand Plain in eastern Minnesota, USA. The climate is continental with cold and long winters and short, warm, and humid summers. For the time period covered in this study, mean annual temperature and mean annual precipitation were 6□C (ranging from ~-12□ in January to ~22□ in July) and ~800 mm, respectively (Cavender-Bares and Reich 2012). The terrain is relatively flat, and soils vary with elevation, with infertile, sandy, and well-drained soils in upland areas and relatively fertile and poorly drained soils in lowland areas. Vegetation is variable, from abandoned croplands to well-preserved vegetation types, like dry oak savannas. A prescribed burning experiment was initiated in the oak savanna in 1964 to characterize responses to varying fire frequency and to restore and maintain oak savanna vegetation (Irving 1970, Peterson and Reich 2001). A 300-ha area was divided into 19 management units of 2.4 to 30 ha, each treated with a burn frequency ranging from nearly annual burns (high-frequency treatment) to complete fire exclusion (unburned treatment) (Irving 1970, Peterson and Reich 2001, Reich et al. 2001). The burn treatments have created a gradient from open savanna to closed forest. Prescribed burns are generally conducted in April or May after snowmelt and before leaf-out; fires are generally low intensity (mean flame lengths of 1 m, Reich et al. 2001b).

Following Cavender-Bares and Reich (2012), we categorized the fire frequency treatments into five levels: unburned (no fire), low frequency or 'Fire 1' (once per decade), medium frequency or 'Fire 2' (2-3 per decade), mid-high frequency or 'Fire 3' (4-5 per decade), and high frequency or 'Fire 4' (7-8 per decade). To measure vascular plant species occurrence and abundance, permanent plots of 0.375 ha (50 m × 75 m) were established within each burn unit. Within each of these 0.375-ha permanent plots, 24 sampling points were established to collect vascular plants species cover percentage with 0.5-m^2 quadrats. Cover values were then summed by species to estimate abundance per species across each 0.375-ha community; thus, species' cover values reflect both their frequency over space (density) and their local abundances (biomass) where they occur (Peterson and Reich 2008, Willis et al. 2010, Cavender-Bares and Reich 2012). Plant surveys were conducted every five years; results from seven surveys spanning five decades are reported here. How a species pool of potential colonists is defined can influence the interpretation of assembly processes driving the structure of local communities (Cavender-Bares et al. 2009, Vamosi et al. 2009, Lessard et al. 2012). In our system, the permanent plots of 0.375 ha occur within an area of ~1000 ha at Cedar Creek and we assume that they share the same regional species pool, minimizing the potential effects of historical processes (Willis et al. 2010, Cavender-Bares and Reich 2012). We set the species pool to include the entire set of species in the oak savanna across any fire regime in a given year (e.g., all species sampled in 2010) to account for the possibility that any species in any fire regime could potentially disperse into any of the burn units within the five-year survey window.

General approach

Our aim was to evaluate both sides of Darwin's naturalization conundrum (i.e., the DNH and PAH) by taking advantage of a long-term, frequently resampled (five-year intervals from 1984 to 2015) fire-frequency experiment that has established a gradient from unburned, dense woodland to frequently burned, open savanna. We evaluated DNH and PAH using taxonomic, functional, and

phylogenetic dimensions of diversity at local and landscape scales. At the local scale, species-level diversity metrics (see below) were estimated within each permanent plot of 0.375 ha (50 × 75 m) across fire experiments ($N = 5$) and for each five-year time interval ($N = 7$). For analysis at the landscape scale, species occurrence ad cover were averaged across all permanent plots.

Nonnative species classification

We defined nonnative species as those that were introduced to the region by humans since early European-American activities (~1850s). Among the 243 vascular plants recorded in all permanent plots, 26 species were identified as nonnative based on these criteria. Note that the occupancy and abundance of nonnative and native plant species vary over time and across fire regimes (Cavender-Bares and Reich 2012), such that some species were not observed in all time intervals or fire treatments (Appendix S1: Fig. S1).

Functional and phylogenetic data

Data for four functional traits (specific leaf area [SLA], seed mass, plant height, and rooting depth)—selected based on the current understanding of key traits related to dispersal, establishment, resource acquisition, and persistence of plants across environmental gradients (Reich 2014, Moles 2017)—were obtained from previous studies (i.e., Willis et al. 2010, Cavender-Bares and Reich 2012, Catford et al. 2019, 2020). Functional traits were measured in the field based on several individuals (between 4 and 6) of each species, except in the case of rare species, for which only one individual was sampled. Individuals were chosen opportunistically among sampling points and species-level trait values were estimated by averaging trait values among individuals (Willis et al. 2010, Cavender-Bares and Reich 2012, Catford et al. 2019, 2020/span>). This trait dataset was not complete, with SLA available for 128 species (52.7% of total), plant height for 143 (58.8%), and rooting depth for 85 (35.0%). We filled these gaps by supplementing the original trait dataset using the TRY (Kattge et al. 2011, 2020) and BIEN (Enquist et al. 2016) databases. In cases where missing traits were not available for a species from these sources, we averaged trait values for all congeners that were available from all sources (Appendix S1: Table S1).

A phylogeny of the 243 observed species was constructed based on the recently published Spermatophyta mega-phylogeny (hereafter SB-tree; Smith and Brown 2018). The SB-tree was reconstructed under a hierarchical framework where individual major clades were first constructed and then placed into two different backbones (i.e., OTB [Open Tree of Life backbone] and MB [Magallón backbone]) and missing taxa were imputed according to relationships in Open Tree of Life (see Smith and Brown 2018 for details). The final SB-tree contains a total of 353,185 and 356,305 species for the OTB and MB backbones, respectively, and to date is the most comprehensive phylogeny for seed plants (Smith and Brown 2018). In this study, we used the SB-tree constructed under the OTB backbone as this tree provides greater resolution towards the tips (Smith and Brown 2018). After checking species names in our community dataset and the pruned SB-tree OTB backbone, we found that 41 species were not represented in the phylogeny, but all of these had congeners in the SB-tree. Thus, we added missing species into the pruned SB-tree using taxonomic constraints (i.e., adding terminal branches at the midpoint of their sister lineages) and estimated branching times under a birth-death model of diversification using the addTaxa package (Mast et al. 2015) in R version 3.4 (R Development Core Team 2018). We repeated the process 1000 times to account for phylogenetic uncertainty in the topology and the final phylogeny used in this study comprises a sample of 1000 fully dichotomous trees. Due to computational demand, we randomly selected a sample of 100 trees and all subsequent analyses were performed using these 100 trees.

Calculation of diversity metrics

Taxonomic diversity was calculated by recording the number, abundance, and identity of species co-occurring with a nonnative focal-species in each permanent plot. We also estimated pairwise species co-occurrence patterns by estimating the normalized checkerboard score (C-Score; Stone and Roberts 1990) between focal nonnative species and the co-occurring species within each plot ($N = 5$) in each fire treatment ($N = 5$) at each time interval ($N = 7$), i.e., 35 matrices per fire treatment for a total of 175. C-Scores are commonly used to quantify species' associations (Gotelli 2000, Bar-Massada 2015). We constructed null models that maintained species' frequency and species richness within communities (i.e., permanent plots) (the trial-swap algorithm; Miklos and Podani 2004) to standardize C-Scores. This was done by calculating standardized effect sizes (SES), comparing an observed value (empirical C-Score) to the mean expected value under a null model (1000 randomizations), while accounting for variance (standard deviation). For standardized C-Scores, positive and negative values denote segregated (negative species associations or competition) and aggregated (positive species associations or facilitation) patterns, respectively, while values close to zero are consistent with random patterns (Callaway and Walker 1997, Tirado and Pugnaire 2005, Bar-Massada 2015).

Using functional and phylogenetic distance matrices as inputs, we calculated multiple metrics accounting for abundance and/or presence-absence of co-occurring species with focal-species within each permanent plot. Prior to calculating functional metrics, a functional distance matrix was constructed using Euclidean distances (all functional traits used are continuous). Metrics included mean pairwise phylogenetic and functional distances (MPD and MFD, respectively) and mean phylogenetic and functional nearest taxon distance (MPNTD and MFNTD, respectively). To facilitate comparisons, we also standardized phylogenetic and functional metrics using standardized effect sizes, with SES values >0 indicating phylogenetic or functional overdispersion and values <0 indicating clustering (Webb et al. 2002). The null model applied was the same used to standardize C-Scores and the statistical significance of each metric was indicated using critical values for a 95% confidence interval ($|SES| > 1.96$) (Pinto-Ledezma et al. 2019). All co-occurring species within each community were included in metric calculations. All calculations were conducted using customized scripts and functions modified from the picante (Kembell et al. 2010), metricTester (Miller et al. 2017b) and ecospat (Di Cola et al. 2017) packages in R.

Presence-absence and abundance-weighted metrics were highly correlated with one another (Appendix S1: Fig. S2); therefore, we only report results for abundance-weighted (aw) metrics because they are more sensitive for detecting shifts in phylogenetic and functional structure (Miller et al. 2017b) and compositional changes over repeated sampling events.

Phylogenetic signal in functional traits

We tested for phylogenetic signal in functional traits using Pagel's λ (Pagel 1999) under a Bayesian approach. Pagel's λ assumes a Brownian motion (BM) evolutionary model and its values range from 0 to 1, with values close to 0 indicating that traits evolved independently of the phylogeny (phylogenetic independence, or no phylogenetic signal) and values close to 1 indicating that traits evolved according to a BM model (equivalent levels of phylogenetic covariance as expected under a BM model, or phylogenetic signal) (Münkemüller et al. 2012, Harmon 2018). We estimated Pagel's λ for the same sample of 100 trees used in previous analyses and ran MCMC chains for 10 million generations, discarding the first million as burn-ins and sampling every 1000 generations in BayesTraits version 3 (available from http://www.evolution.rdg.ac.uk/). Before this analysis, traits were log-transformed to meet the assumption of normality (Harmon 2018). We additionally estimated Pagel's λ under a maximum likelihood approach and calculated values for Blombrg's K (Blomberg et al. 2003). Both of these analyses produced results similar to those observed the Bayesian analysis of Pagel's λ; we present only the latter for simplicity.

Statistical analyses

To evaluate the probability of changes in relatedness/similarity of focal-nonnative species to recipient communities through time (1984-2015) and across fire regimes (unburned to high-frequency), we modeled focal-species (for the three dimensions of diversity) as a function of fire regime (5 levels) and time interval (7 levels) using a Bayesian Multilevel Modeling (MLMs) framework (Gelman and Hill 2007, Finch et al. 2014). Using MLM models allowed for analysis of focal-species metrics nested within hierarchical sampling units (fire experiments and time periods) (Finch et al. 2014). We used a bivariate tensor spline (Wood et al. 2013) to model interaction effects of unknown, potentially non-linear form on focal-species relatedness (Bürkner 2017). MLMs were performed for all nonnative species together and for major taxonomic groups (i.e., dicots and monocots). In total, we constructed six models (3 levels × 2 metrics) related to changes in within-focal-species abundance and richness, 12 (3 levels × 4 metrics) related to changes in phylogenetic relatedness, and 12 (3 levels × 4 metrics) related to changes in functional similarity. In addition, given that environmental stressors like fire (or its absence) can influence species coexistence, we built several models in which species relatedness within fire experiments was a function of time intervals. This allowed us to explore how focal-species responded to environmental conditions over time. All MLMs were run using 4 NUTS sampling chains for 5000 generations, discarding 20% of each run as burn-ins, using the R package brms (Bürkner 2017), which implements Bayesian MLM in R using the probabilistic programming language Stan (Carpenter et al. 2017). We also used Bayes Factors (BF; Kass and Raftery 1995) for pairwise comparisons.

We used permutational multivariate analysis of variance (PERMANOVA, Anderson 2001) to evaluate the uncertainty—the lack of complete knowledge about a parameter—associated with the imputation of missing species in the phylogenies. To do so, we modelled MPD/MPNTD as a function of fire regimes (5 levels) and time intervals (7 levels), using focal-species identities as random variables ($N = 26$) and phylogenetic trees ($N = 100$) as replicates. Under this modeling framework, the variance not explained by individual factors and their interactions can be attributed to differences resulting from phylogenetic uncertainty caused by species imputation (Rangel et al. 2015).

Results

General description of the data

Within communities and treatments, native and nonnative species exhibited similar trait values to each other (Appendix S1: Fig. S3). Statistical comparison showed negligible evidence for differences in trait values between these two species categories (i.e., natives versus nonnatives; SLA [BF = 0.27], plant height [BF = 0.27], rooting depth [BF = 0.61], and seed mass [BF = 0.22]) (Appendix S1: Fig. S3). Despite the lack of systematic differences between natives and nonnatives, trait values did vary considerably among all species (Appendix S1: Fig. S4). In addition, while imputation of missing species in phylogenetic trees has been considered an important source of phylogenetic uncertainty in comparative studies, our results show that species imputation contributed little of the total variation in phylogenetic structure of focal-nonnative species (awMPD = 4.95%, awMPNTD = 10.10%). Most of the variation was instead attributable to evolutionary and ecological patterns of interest, i.e., phylogenetic and functional correlations among co-occurring species.

Phylogenetic signal in functional traits

Phylogenetic signal exhibited intermediate to high λ values (Fig. 3; though λ was weak for SLA), suggesting that trait values of

species co-occurring in plots were similar, though not to the extent expected under a Brownian motion model of evolution (= 1; Fig. 3). These results were consistent across all 100 phylogenetic trees, i.e., regardless of phylogenetic uncertainty introduced by missing terminal branches.

Patterns of taxonomic, phylogenetic, and functional structure of nonnative focal-species

Species co-occurrence of focal nonnatives—measured as the tendency of focal species to occur in species-rich or species-poor communities—varied considerably among the 26 focal species (Appendix S1: Fig. S5A-D). We found evidence for differences in species co-occurrence (abundance and richness) of focal nonnatives with their recipient communities for dicots (Appendix S1: Fig. S5 A and C; BF = 323.76 and BF = 3498.19 for abundance and richness, respectively) but not for monocots (Appendix S1: Fig. S5 B and D; BF = 0.34 and BF = 0.48 for abundance and richness, respectively). Co-occurrence patterns based on C-Scores also indicated high variability among focal species, but not significant differences in species-pairs associations between dicots and monocots (Appendix S1: Fig. S5E-F; BF = 0.24 for dicots and BF = 0.18 for monocots). Despite the lack of evidence for differences between species pairs, patterns of aggregation and segregation were observed between nonnatives and native species in recipient communities (Appendix S1: Fig. S5E-F). For example, *Poa pratensis* (Kentucky bluegrass), which occurred in species-rich and abundant communities (Appendix S1: Fig. S5B-D), also tended to co-occur with species with which it may have had positive interactions (i.e., negative SES C-Score; Appendix S1: Fig. S5-F).

In general, co-occurrence patterns for focal nonnative species varied strongly across both phylogenetic and functional dimensions (Fig. 4). All possible patterns were observed, e.g., greater co-occurrence with: i) closely related but functionally distinct species (e.g., *Pyrus malus* [paradise apple] [Fig. 4A and 4E] with *Digitaria sanguinalis* [hairy crabgrass] [Fig. 4B and 4F]); ii) distantly related but functionally similar species (e.g., *Glechoma hederacea* [ground ivy] [Fig. 4A and 4E] with *Setaria viridis* [green bristlegrass] [Fig. 4B and 4F]); iii) closely related and functionally similar species (e.g., *Linaria vulgaris* [yellow toadflax] [Fig. 4A and 4E] with *Phleum pretense* [timothy-grass] [Fig. 4B and 4F]); and iv) distantly related and functionally distinct species (e.g., *Plantago major* [broadleaf plantain] [Fig. 4A and 4E]). Despite this high degree of variation, there was no evidene for differences in the patterns of phylogenetic structure among dicots and among monocots (Fig. 4; BFs = 1.07 for dicots and 2.03 for monocots) or in functional structure (BFs = 0.27 for dicots and 2.03 for monocots).

At the landscape scale, phylogenetic and functional metrics did not significantly differ from expectations under null models (Fig. 4), suggesting stochastic patterns of co-occurrence of nonnative species in recipient communities. However, at local scales we did detect significant deviations from null expectations (Appendix S1: Fig. S6 and S7). For instance, the most common monocot and dicot species (*Poa pratensis* and *Polygonum convolvulus* [black bindweed]) showed significant phylogenetic clustering in 31% and 17% of all plots, respectively, whereas no significant phylogenetic overdispersion was observed (Appendix S1: Fig. S6). Additionally, in these same recipient communities, both *Poa pratensis* and *Polygonum convolvulus* tended to co-occur more with functionally distinct species (overdispersion of traits, Appendix S1: Fig. S7). In addition, local-scale patterns showed shifts from overdispersion to clustering, and vice versa, across fire gradients and time periods for both phylogenetic and functional measures, indicating that co-occurrence patterns were dynamic over space and time across multiple axes of diversity (Appendix S1: Fig. S6 and S7).

Effects of fire regimes and time on co-occurrence patterns of focal nonnatives

For all three dimensions of diversity, the individual and combined effects of fire frequency and time were non-linear (Figs. 5 and 6).

Focal nonnatives tended to co-occur more in species-abundant (left panels in Fig. 5) and species-rich communities (middle panels in Fig. 5) with increasing fire frequency, though co-occurrence peaked at intermediate fire frequencies for some groups, e.g., abundance response of nonnative dicots (Fig. 5D). Pairwise co-occurrence patterns (C-Scores) showed complex, nonlinear patterns across fire treatments (right panels in Fig. 5), with positive associations found in the unburned and frequently burned treatments, and negative associations under intermediate fire frequencies. Notably, both dicot and monocot nonnatives responded similarly to fire gradients (Fig. 5, panels D to I).

Bayesian MLMs revealed a complex nonlinear response of focal nonnatives' phylogenetic/functional structure patterns to fire frequency (Fig. 6). These results were consistent regardless of phylogenetic scale (all species or dicots and monocots analyzed separately) and metric (awMPD/MFD, awMPNTD/MFNTD). Overall, there were changes from overdispersion to clustering in functional traits, with nonnative species tending to co-occur more with functionally similar species under increasing fire frequency (right-hand panels in Fig. 6). Furthermore, for the phylogenetic dimension, MLMs provided evidence for nonlinear changes in the phylogenetic structure of focal nonnatives in native communities with increasing fire frequency (left-hand panels in Fig. 6). Phylogenetic clustering was highest in communities subjected to low fire frequency, and phylogenetic overdispersion was greatest under intermediate and high-fire regimes, albeit with a return to phylogenetic clustering at medium-high fire regimes. Note that based on MPNTD, phylogenetic overdispersion was greatest under intermediate and high fire regimes (Fig. 6B).

Increased clustering of traits with increasing fire frequency was consistent over time (Fig. 7 bottom panels). The phylogenetic dimension also revealed a complex temporal pattern (Fig 7. top panels). Although focal nonnatives tended to co-occur more with closely related species in unburned plots and with distantly related species in frequently burned plots, there were interannual changes in phylogenetic structure of nonnative species (Fig. 7). For example, there was a change from clustering to overdispersion in unburned plots in 2000 (Fig. 7 top-left panel), which may indicate that external factors (e.g., interannual climate variability) influenced co-occurrence patterns of focal nonnative species.

Discussion

The temporal dynamics of co-occurrence patterns of nonnative species in invaded oak savanna communities across a long-term experimental fire gradient revealed that neither of Darwin's naturalization hypothesis nor the pre-adaptation hypothesis fully explained invasion dynamics. Applying our focal-species approach to three different dimensions of vascular plant diversity (taxonomic, phylogenetic, and functional), we found that co-occurrence patterns of 26 nonnative focal species (Appendix S1: Fig. S1) did not follow a general tendency of clustering (i.e., supporting the pre-adaptation hypothesis) or overdispersion (i.e., supporting Darwin's naturalization hypothesis) (Fig. 4). Rather, we found that community assembly was influenced by species' differences in evolutionary history (i.e., shared ancestry) and by ecological differences associated with functional traits that ultimately regulate the colonization and persistence of nonnatives within invaded communities (Fig. 1C). Altogether, our findings provide insights for understanding the invasion dynamics of native communities across environmental gradients and at multiple temporal and spatial scales in a highly diverse ecosystem of North America.

Multiple processes have been proposed to explain introduced species' success outside their native ranges (Gallien and Carboni 2017, Cadotte et al. 2018, Redding et al. 2019). Prior studies have reported contrasting results in terms of phylogenetic relatedness of nonnative species to recipient assemblages (Carboni et al. 2013, Li et al. 2015, Marx et al. 2016), with mixed support for both hypotheses comprising Darwin's naturalization conundrum (Kusumoto et al. 2019). Our results show differential patterns of relatedness of focal nonnative species to recipient native communities, with some nonnatives co-occurring more with closely related

natives (supporting the pre-adaptation hypothesis), and others with distantly related natives (supporting the naturalization hypothesis) (Fig. 4 upper panel). These results suggest that different assembly processes—e.g., biotic interactions, environmental filtering—have simultaneous effects on focal nonnative co-occurrence patterns (Boulangeat et al. 2012, Gallien and Carboni 2017, Kusumuto et al. 2019; see also Fig. 1C).

Evaluating the taxonomic dimension, we found that both positive and negative interactions appeared to be important in the co-occurrence of nonnative species with native species (Appendix S1: Fig. S5E-F). Functional patterns differed from those observed for the phylogenetic dimension (Fig. 4 lower panel). This may indicate that functional traits are modulating co-occurrence patterns between nonnative and native species (Marx et al. 2016, Carboni et al. 2018, Catford et al. 2016, 2019), by controlling or regulating species' responses to different assembly processes (Cavender-Bares et al. 2004, Swenson and Enquist 2009, Pinto-Ledezma et al. 2018). For example, similarity in ecologically relevant traits of closely related species should result in patterns of phylogenetic clustering under similar environmental conditions, while similarity in distantly related species would be associated with a pattern of phylogenetic overdispersion (Cavender-Bares et al. 2004, 2009). In other words, evolutionary conservatism and convergence of functional traits help to explain why nonnative species tend to co-occur with closely related natives (as suggested by PAH) and distantly related natives (as suggested by DNH), respectively (Fig. 1C). Indeed, we found that functional trait values in co-occurring species at Cedar Creek were similar 3). In addition, trait similarity between native and nonnative species (Appendix S1: Fig. S3) might suggest that nonnative species have associated traits (both functional and ecological) that made them preadapted to succeed in the communities they invaded (Fig. 3, van Kleunen et al. 2010, Pearson et al. 2018), a pattern that is expected to emerge over time due to environmental selection on evolutionarily conserved traits.

Environmental conditions and disturbances constrain patterns of species diversity within communities by acting as filters that alter species co-occurrence patterns (Connell 1978, Peterson and Reich 2008, Pinto-Ledezma et al. 2018). Disturbances such as fire can generate stressful environmental conditions in which only a subset of tolerant species will recruit and persist, thereby diminishing the strength of density-dependency interactions (Shea et al. 2004, Peterson and Reich 2008, HilleRisLambers et al. 2012, Coyle et al. 2014). These factors also influence the degree to which nonnative species co-occur with natives in invaded communities (Shea and Chesson 2002, Thuiller et al. 2010, Cadotte et al. 2018). Our results show that fire frequency generated idiosyncratic effects on co-occurrence patterns in invaded communities (Fig. 6), indicating the simultaneous and interacting effects of assembly processes across environmental gradients—i.e., as environmental conditions changed, density-dependent interactions promoted the coexistence of some species while excluding others (Chesson and Huntly 1997, Germain et al. 2018). In fact, we found that focal nonnatives became more functionally similar to natives with increasing fire frequency, which might suggest a strong influence of environmental filtering (Fig. 6 right panels). However, phylogenetic distance exhibited a complex nonlinear trend (Fig. 6 left panels), matching our third prediction (Fig. 2C). Specifically, non-natives were more closely related to natives in communities with low fire frequency (Fire 1). Shifts to phylogenetic overdispersion appeared under medium-high fire frequency, possibly as a consequence of competitive interactions (Fig. 6). In other words, both environmental filtering and biotic interactions acted in concert to shape co-occurrence patterns of nonnative species across environmental gradients. This is consistent with prior experimental studies (e.g., Germain et al. 2018) highlighting the importance of simultaneous effects of environmental filtering and competitive interactions on community assembly (Chesson and Huntly 1997, Chesson 2000, Ackerly 2003, Germain et al. 2018).

Species composition and structure within communities is dynamic in space and time, varying from short timeframes at small scales (e.g., Appendix S1: Fig. S1) to millions of years across biogeographical regions (Chesson 2000, Williams et al. 2004, Cavender-Bares and Reich 2012, Pinto-Ledezma et al. 2018, 2019). Thus, a better understanding of invasion dynamics and their

relationship to DNC requires evaluation across multiple temporal scales. Indeed, recent evidence indicates that a single snapshot in time could mislead interpretations on both sides of Darwin's conundrum (Li et al. 2015, Cadotte et al. 2018) or prevent observation of the full range of impacts of nonnative species on invaded communities (Gilbert and Levine 2013). Our results support these time-dependent findings, as we found shifts over time in the phylogenetic and functional co-occurrence structure of focal nonnatives across the fire frequency gradient (Appendix S1: Fig. S6 and S7). For example, *Poa pratensis*, the most common and abundant nonnative species in our study system (Appendix S1: Fig. S1), tended to co-occur more with closely related species, supporting the PAH (Fig. 4B); however, in plots protected from fire, phylogenetic clustering from 1984 to 2005 gave way to phylogenetic overdispersion in 2010 and 2015 (Appendix S1: Fig. S6). Thus, depending on the time periods considered, the co-occurrence patterns of *Poa pratensis* could support PAH or DNH. These findings highlight the importance of examining time series in the study of biological invasions, given that co-occurrence patterns are an emergent characteristic of dynamic population changes across many species (Chesson 2000, Cavender-Bares and Reich 2012, Li et al. 2015). Indeed, an observed species may be only fleetingly present in a community, confounding inferences based on a single time point (Gilbert and Levine 2013, Germain et al. 2018).

Given that invasion is a dynamic process, nonnative species need to surpass different biotic and abiotic filters to become naturalized (i.e., reproduce and maintain viable populations over time; Richardson et al. 2000). The invasion stage (i.e., introduction, establishment, or naturalization and spread) can also influence co-occurrence patterns of nonnative species in invaded communities (Richardson et al. 2000, Kolar and Lodge 2001, Li et al. 2015, Catford et al. 2019). Still, the degree to which nonnative species interact with native species in each invasion stage further depends on associated species traits (Shea and Chesson 2002, Carboni et al. 2018, Catford et al. 2019), as well as the physical environment and disturbance regimes in invaded communities (Cavender-Bares and Reich 2012, Catford et al. 2016, 2020). For example, traits related to dispersal capacity (e.g., seed mass) could be more relevant for colonization and spread (Tilman 1994, Catford et al. 2016) and resource economics traits for establishment or naturalization (Reich 2014, Catford et al. 2016, Díaz et al. 2016, Kunstler et al. 2016). Similarly, disturbances may alter interactions between native and nonnative species and thus influence species' relative fitness in invaded communities (Cavender-Bares and Reich 2012, Catford et al. 2016, 2020). Our results show that functional trait values of natives and nonnative species in Cedar Creek were relatively similar (Appendix S1: Figs. S3 and S4), a pattern that was consistent across fire gradients (Peterson and Reich 2008, Cavender-Bares and Reich 2012). For example, in communities subjected to high-fire frequency that were dominated by grass and forb species, seed mass values were similar among co-occurring native (e.g., *Andropogon gerardii* [big bluestem] and *Schizachyrium scoparium* [little bluestem]) and nonnative (e.g., *Agropyron repens* [quackgrass]) species (Appendix S1: Fig. S4). This suggests that species with strong dispersal capacity are able to colonize and reproduce in communities that are not reached by weak dispersers and potentially strong competitors (e.g., shade-tolerant and fire-sensitive species) (Tilman 1994, Shea and Chesson 2002). Taken together, these findings indicate that trait similarity among native and nonnative species and their interactions and responses to the physical environment all influence the process of invasion across environmental gradients.

Finally, physical environment plays a crucial role in structuring plant communities (e.g., Šímová et al. 2015, Pinto-Ledezma et al. 2018, Keil and Chase 2019, Harrison et al. 2020). Both native and nonnative species respond to the physical environment of the communities they occupy, determining community structure and composition (Chesson 2000, Shea and Chesson 2002, Pearson et al. 2018, Harrison et al. 2020). Our findings are consistent with a large body of theory (e.g., Šímová et al. 2015, Pinto-Ledezma et al. 2018, Harrison et al. 2020 and references therein) showing that environmental conditions act as strong selective forces that filter species with similar trait values (Figs. 6 and 7). In fact, recent studies of invasiveness at different spatial scales and of different taxa demonstrate that the physical environment is one of the main drivers of establishment of nonnative species (González-Moreno et al.

2014, Dawson et al. 2017, Kusumoto et al. 2019, Redding et al 2019). Thus, given that the processes driving species distributions and co-occurrence patterns are scale-dependent (Leibold et al. 2004, Cavender-Bares et al. 2009, Keil and Chase 2019, Harrison et al. 2020), assessments of long-term time series data at multiple spatial scales are necessary to comprehensively understand the causes of species invasions and their consequences on recipient communities (Pauchard and Shea 2006, Milbau et al. 2009, Thuiller et al. 2010, Gallien and Carboni 2017, Catford et al. 2019). These efforts would contribute as ecological basis for enhancing the development of management strategies of biodiversity in the Anthropocene.

The focal-species approach

The term focal-species has been used previously, e.g., defined as a targeted species for conservation and management purposes (Lambeck 1997) and is conceptually similar to the niche concept (Pickett and Bazzaz 1978), which can be interpreted as differences in functional traits between a given species and those of co-occurring species (Pickett and Bazzaz 1978, Ackerly and Cornwell 2007). The focal-species approach as extended here: 1) allows evaluation of phylogenetic and functional distances between the focal species and co-occurring species, thus permitting the assessment of the potential community-level consequences of 'focal species' interactions as well as the influence of community-wide interactions on the focal species; 2) is advantageous for incorporating different dimensions of biodiversity (i.e., taxonomic, functional, phylogenetic); 3) can be adapted to different spatial and temporal scales; and 4) facilitates consideration of environmental factors in driving species co-occurrence (Villalobos et al. 2013, 2016, Barnagaud et al. 2014, Herrera-Alsina and Villegas-Patraca 2014, Miller et al. 2017a).

Extending the diversity fields' framework to focal-species under a combined phylogenetic and functional perspective (Box 1) offers an innovative way to evaluate patterns of species-level co-occurrence at local scales, enhancing our understanding of the mechanisms driving invasion dynamics in natural communities. For example, by combining different dimensions of vascular plant diversity under the focal-species framework, we were able to detect shifts in the phylogenetic relatedness and functional similarity of focal nonnatives with respect to recipient communities across environmental gradients and over time. This is particularly important given that individual species, including nonnatives, respond differently to changes in environmental conditions of local communities (Tilman 2004, Ackerly and Cornwell 2007, Li et al. 2015, Redding et al. 2019). Further analyses addressing different taxa, biogeographical regions, or environmental conditions could reveal more insights about the mechanisms driving co-occurrence of nonnative species in recipient communities or elucidate the role of other axes of variation shaping species co-occurrence patterns. Finally, the integration of multiple dimensions of biodiversity within the focal-species framework can enhance our ability to produce reliable information on species co-occurrence at different spatial and temporal scales, facilitating our abiity to monitor changes in both individual species and whole communities, and thus helping to guide conservation efforts.

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Statement of authorship

JC-B, JNP-L and DJL conceived the ideas presented and tested herein. JNP-L managed the project. JNP-L performed the analyses

and wrote the first draft. FV, JAC and PBR contributed to the ideas and interpretation of data, and all authors contributed throughout the whole writing process. PBR has co-led the implementation and management of the long-term fire frequency experiment and associated community censusing and data curation.

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BOX 1. The focal-species approach

Species co-occurrence patterns in local communities are a consequence of ecological processes (species interactions with other organisms and the environment) and historical processes (biogeographic history, long-term dispersal, past diversification) that operate over short and long time scales, respectively (Cavender-Bares et al. 2016, 2018, Pinto-Ledezma et al. 2019). Different metrics have been used to measure the degree of relatedness/similarity (see Miller et al. 2017, Scheiner et al. 2017) of species co-occurring within local communities to infer assembly processes from community phylogenetic/functional structure (Cavender-bares et al. 2006, Mayfield and Levine 2010). These metrics are calculated using a community data matrix (CDM)—in which rows are communities and columns are species—in combination with a distance matrix, either phylogenetic or functional. Generally, CDMs are analyzed by rows (*Q*-mode in Arita et al. 2008, see also Villalobos and Arita 2010), summarizing information at the community level. However, CDMs can also be analyzed by columns (*R*-mode in Arita et al. 2008, Villalobos and Arita 2010), summarizing information at the species level. In addition, by intersecting rows and columns (*Qr*-mode and *Rq*-mode in Arita et al. 2008), it is possible to obtain new information, e.g., the 'diversity field' of a given species (Arita et al. 2008), which represents the species richness of communities within the distribution of a species. This can be interpreted as the tendency of a given species to occur in

species-rich or species-poor communities, i.e., to coexist with many or with few species (Villalobos and Arita 2010).

Building on this framework, Villalobos et al. (2013, 2017) extended the concept of diversity fields—the set of diversity values of sites within the geographical range of a given species (Arita et al. 2008)—to 'phylogenetic fields' (Villalobos et al. 2013) and 'functional fields' (Villalobos et al. 2017, see also Miller et al. 2017) that describe the overall phylogenetic/functional structure of species co-occurring with a given species geographical range. These fields are interpreted as the tendency of a focal species to co-occur either with closely related/functionally similar or distantly related/functionally dissimilar species (Villalobos et al. 2013, 2017). Similarly, phylogenetic/functional fields can be used as metrics of species-level coexistence. All three of these approaches—diversity, phylogenetic, and functional fields—are usually applied at macroecological scales (Arita et al. 2008, 2010, Villalobos and Arita 2010, Villalobos et al. 2013, 2016, 2017) with some local-scale exceptions (e.g., Herrera-Alsina & Villegas-Patraca 2014, Miller et al. 2017a, Kusumoto et al. 2019). Given that the observational units in our study are species within local communities, we downscale the concept of fields applied at large geographical scales to local communities in which phylogenetic/functional structure is measured on the set of species that co-occur with a focal species in a particular community (Fig. 1A-B). This extension enables evaluation of co-occurrence patterns and inferences regarding assembly processes to be applied at the level of individual species rather than entire commuities. In doing so, we obtain separate estimates for each species occurring in a local community rather than a single mean across all species co-occurring in a community (Fig. 1A-B).

BOX 2. Changes in species' functional traits along Cedar Creek's fire frequency gradient

Across fire gradients within the Cedar Creek system, plant height and tree cover are generally negatively associated with fire frequency, such that overstory tree cover decreases and understory light availability increases in areas with more frequent fires (Reich et al. 2001, Peterson and Reich 2008, Willis et al. 2010). SLA is predicted to decrease with increasing light availability in the oak savanna. In the understory of unburned dense forest canopies, high SLA maximizes light interception. In contrast, in frequently burned open areas prone to high solar radiation and desiccation, low SLA, which is associated with high leaf hydraulic resistance, limits plant desiccation (Givnish and Vermeij 1976, Ackerly 2004). Similarly, seed mass tends to decline with increasing fire frequency. Larger seeds are able to establish and survive as seedlings in competitive communities with low light availability, whereas small seeds are able to disperse further and to reproduce in large numbers, allowing small-seed species to colonize patches that are not reached by large-seeded species (Tilman 1994; Leishman et al. 1995, Moles et al. 2005). Conversely, rooting depth tends to increase with increasing fire frequency, given that deeper roots enhance access to groundwater resources and increase plant recovery after fire disturbance (Peterson and Reich 2008, Willis et al. 2010, Pierret et al. 2016).

FIGURE LEGENDS

Fig. 1. Conceptual framework for the estimation of phylogenetic/functional structure of focal-species contrasted with the traditional estimation of phylogenetic/functional structure at the community level. Here we show the difference between estimates for standard mean pairwise phylogenetic distance (MPD) between species occurring within a community (a single, community-level value) and MPD_{focal} (multiple, species-level values). Again, while traditional MPD is calculated based on the mean distance among all possible pairs of species within a community, MPD_{focal} is based on the mean distance of a focal species relative to the co-occurring species in

a local community (e.g., nonnative species in A and B). Under this simple framework, it is possible to evaluate both the phylogenetic relatedness and functional similarity of nonnative species in native communities and consequently conduct a more comprehensive analysis of both sides of Darwin's naturalization conundrum (C). (A) Darwin's naturalization hypothesis (DNH): nonnative species closely related to native species are less likely to successfully invade native communities because they share similar and already occupied niches (continuous boxes in panel C). (B) Pre-adaptation hypothesis (PAH): nonnatie species closely related to native species should be favored because they share similar traits with native species, making them well-suited ("preadapted") to the novel range, and permitting them to colonize and further adapt (dashed boxes in panel C). Panel C adapted from Cavender-Bares et al. (2004).

Fig. 2. Hypotheses and predictions for co-occurrence patterns of focal-nonnative species with resident species in invaded communities across environmental gradients at Cedar Creek. The curves depict theoretical expectations of changes in phylogenetic/functional structure across fire and light-availability gradients, explained in the main text. Note that each panel correspond to the each prediction explained in the introduction section, for example, the panel A) correspond to the prediction 1.

Fig. 3. Bayesian phylogenetic signal estimated using Pagel's □ and a sample of 100 phylogenetic trees. Posterior probability distributions of (A) specific leaf area, (B) plant height, (C) rooting depth, and (D) seed mass. Posterior distribution (and 95% confidence interval, vertical gray dotted lines) show □ values from 10 million generations sampled every 1000 generations. Vertical dashed gray lines represent the mean □ value estimated under a maximum likelihood approach over a sample of 100 trees.

Fig. 4. Patterns of phylogenetic relatedness and functional similarity of focal nonnative species relative to native species in invaded communities for 26 nonnative species found in oak savanna permanent plots at the Cedar Creek Ecosystem Science Reserve, USA. Values correspond to abundance-weighted metrics averaged across all permanent plots (landscape scale) for both phylogenetic (top panel) and functional dimensions (bottom panel), where positive and negative metric values can be interpreted as overdispersion and clustering, respectively. Panels A-B and C-D correspond to the standardized effect size–mean phylogenetic distance (SES-MPD_{focal}nd the standardized effect size–mean phylogenetic nearest taxon distance (SES-$MPNTD_{focal}$), respectively and panels E-F and G-H to the standardized effect size–mean functional distance (SES-MFD_{focal}) and the standardized effect size–mean phylogenetic nearest taxon distance (SES-$MFNTD_{focal}$), respectively. See calculation of diversity metrics in the methods section and Box 1 for further details.

Fig. 5. Marginal effects plots of changes in the taxonomic dimension across the fire gradient. Continuous blue lines represent fitted slopes (with 95% confidence intervals in gray) smoothed over the fire-frequency gradient from the Bayesian MLMs. The left-hand and middle columns show the variation of species co-occurrence of focal nonnatives for abundance and richness metrics, respectively, estimated as the tendency of focal nonnatives to occur in species-rich or species-poor communities. The right-hand column shows the variation of focal species co-occurrence using the C-Score metric. Note that at both extremes of the fire frequency gradient (i.e., unburned and frequent-fire treatments), nonnatives tended to co-occur with native species under positive interactions. Also, Bayesian MLMs showed similar patterns for dicots and monocots, confirming that nonnative plant species responded in similar ways to fire regimes and tht patterns were not driven by simple differences between tree versus grass species.

Fig. 6. Marginal effects plots of changes in phylogenetic structure and functional structure of focal nonnative species in recipient communities across the fire frequency gradient. Continuous blue lines represent the fitted slopes (with 95% confidence intervals in gray) smoothed over the fire-frequency gradient from Bayesian MLMs. Left-hand columns (A, B, E, F, I and J) show the variation in focal nonnative species co-occurrence in recipient communities for the phylogenetic dimension and the right-hand columns (C, D, G, H, K and L) for the functional dimension. The *y*-axes for all panels represent fitted abundance-weighted metrics values (MPD/MFD and MPNTD/MFNTD) across the fire frequency gradient, where positive and negative metric values can be interpreted as overdispersion and clustering, respectively. See calculation of diversity metrics in the methods section for details of metric calculations.

Fig. 7. Fitted metric values from Bayesian MLMs over time for the two extreme ends of the fire frequency gradient, i.e., unburned and fire 4 treatments. Upper and lower panels correspond to phylogenetic and functional dimensions, respectively. The *x*-axes for all panels represent fitted abundance-weighted metrics values (MPD/MFD) across the fire frequency gradient, where positive and negative metric values can be interpreted as overdispersion and clustering, respectively.

Fig. 1

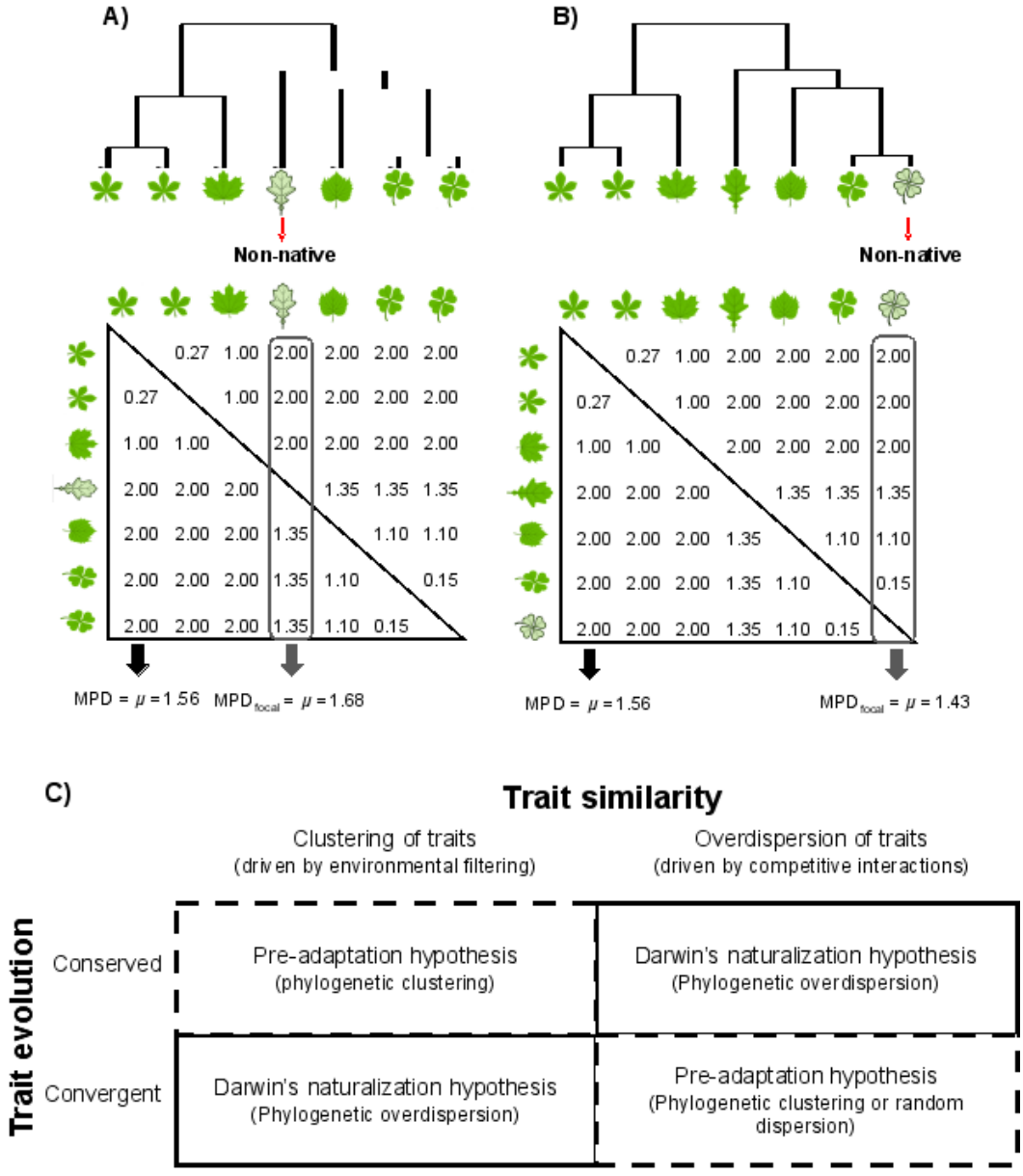

A)
Non-native
0.27 1.00 2.00 2.00 2.00 2.00
0.27 1.00 2.00 2.00 2.00 2.00
1.00 1.00 2.00 2.00 2.00 2.00
2.00 2.00 2.00 1.35 1.35 1.35
2.00 2.00 2.00 1.35 1.10 1.10
2.00 2.00 2.00 1.35 1.10 0.15
2.00 2.00 2.00 1.35 1.10 0.15
MPD = μ = 1.56
MPD focal = μ = 1.68
B)
Non-native
0.27 1.00 2.00 2.00 2.00 2.00
0.27 1.00 2.00 2.00 2.00 2.00
1.00 1.00 2.00 2.00 2.00 2.00
2.00 2.00 2.00 1.35 1.35 1.35
2.00 2.00 2.00 1.35 1.10 1.10
2.00 2.00 2.00 1.35 1.10 0.15
2.00 2.00 2.00 1.35 1.10 0.15
MPD = μ = 1.56
MPD focal = μ = 1.43
C)
Trait similarity
Clustering of traits
(driven by environmental filtering)
Overdispersion of traits
(driven by competitive interactions)
Trait evolution
Conserved
Pre-adaptation hypothesis
(phylogenetic clustering)
Darwin's naturalization hypothesis
(Phylogenetic overdispersion)
Convergent
Darwin's naturalization hypothesis
(Phylogenetic overdispersion)
Pre-adaptation hypothesis
(Phylogenetic clustering or random dispersion)

Fig. 2

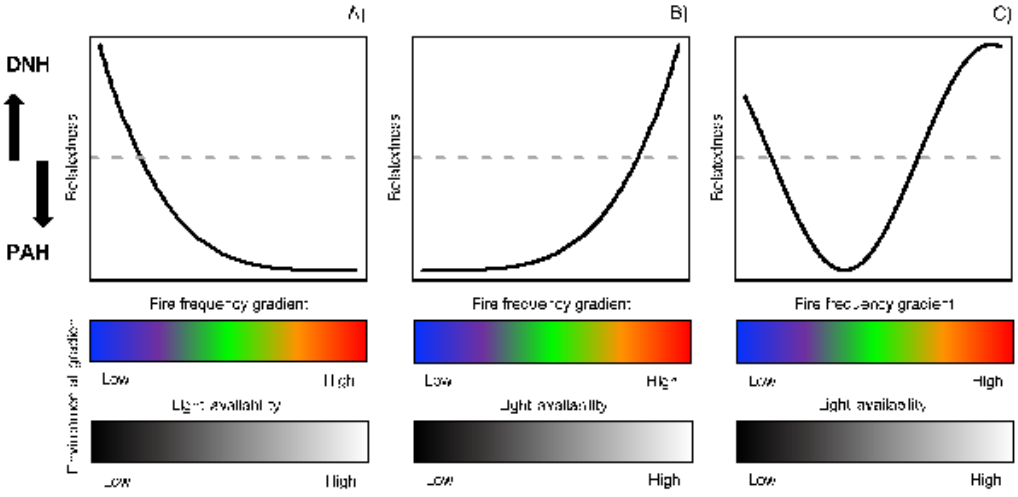
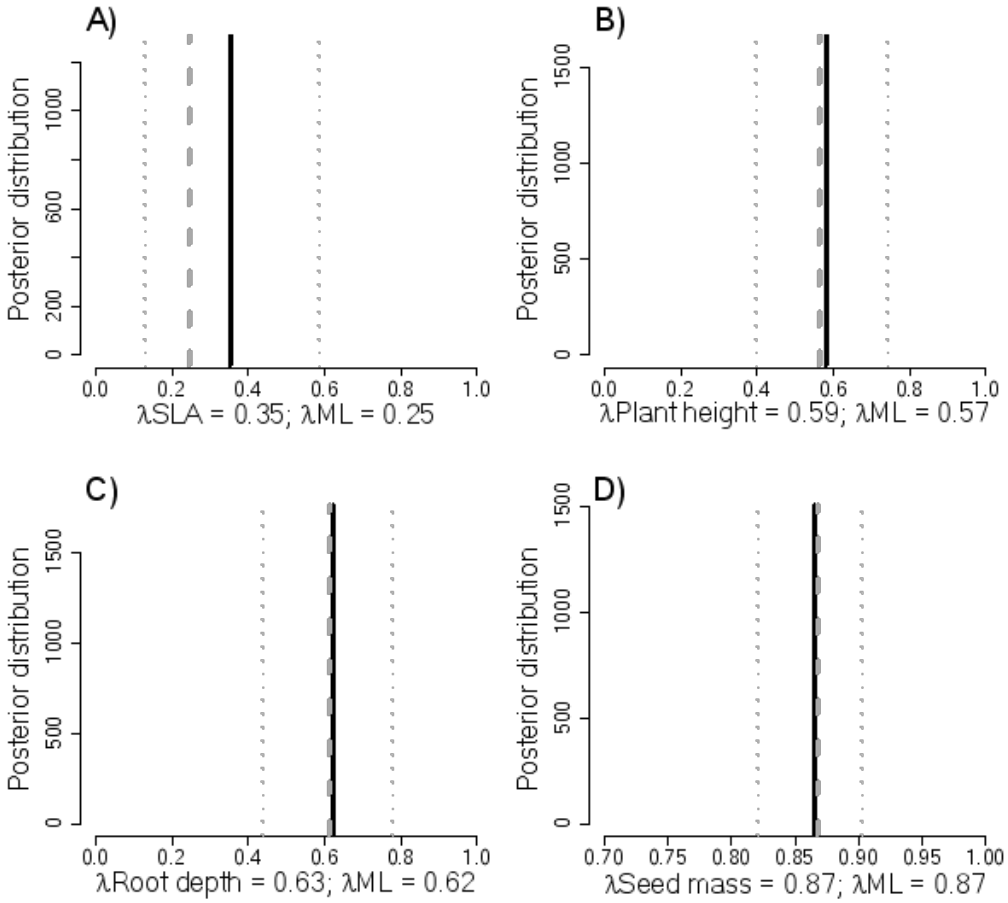

A)
B)
C)
DNH
PAH
Relatedness
Fire frequency gradient
Low
High
Light availability
Low
High

Fig. 3



Note: We did not evaluate the phylogenetic signal of functional trait combinations (i.e., LHS and LHS + root depth) given the expectation that traits evolve independently of one another

Fig. 4

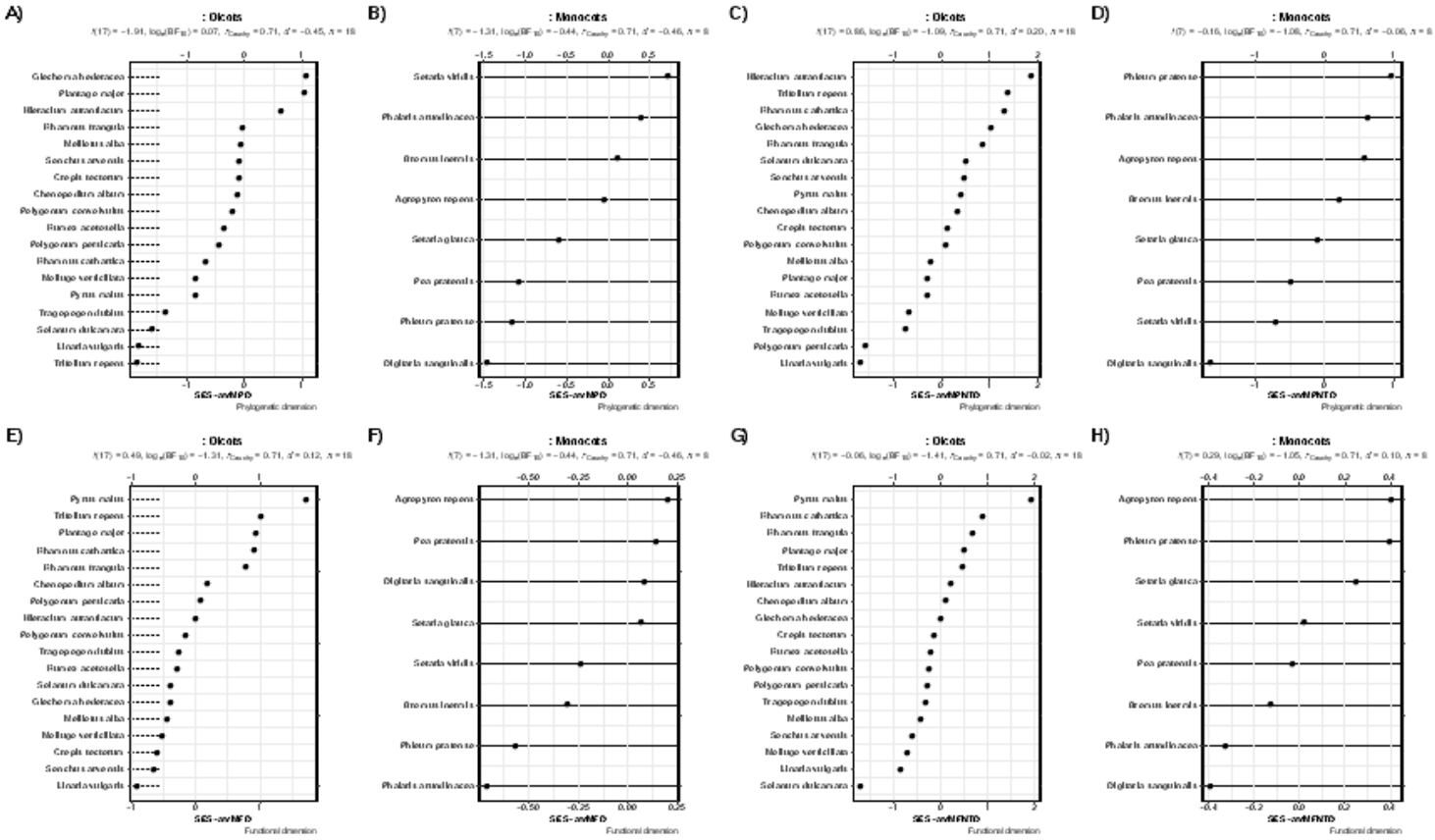

A)
: Dicots
B)
: Monocots
C)
: Dicots
D)
: Monocots
E)
: Dicots
F)
: Monocots
G)
: Dicots
H)
: Monocots
SES−avMPD
SES−avMPNTD
Phylogenetic dimension
Functional dimension

Fig. 5

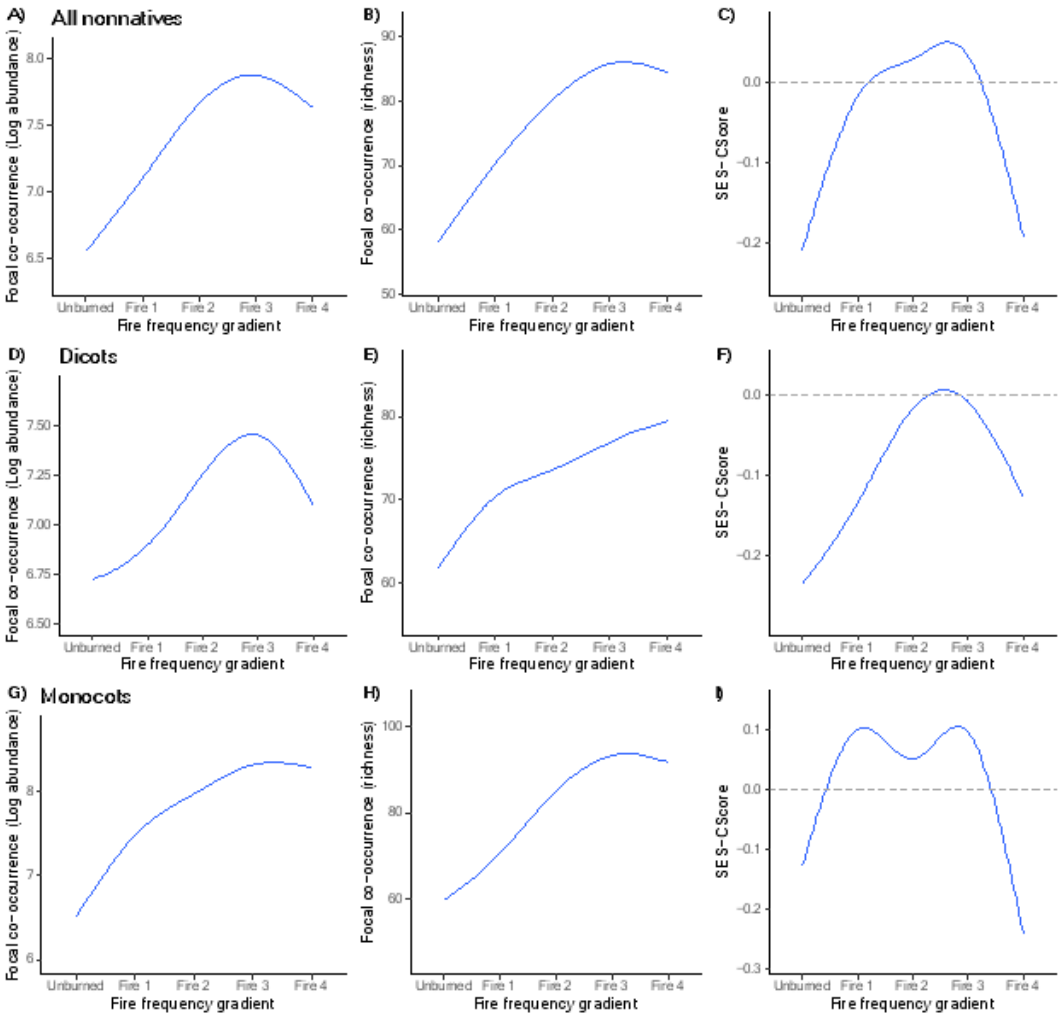

A)
All nonnatives
B)
C)
D)
Dicots
E)
F)
G)
Monocots
H)
I)
Focal co-occurrence (Log abundance)
Focal co-occurrence (richness)
SES-CScore
Unburned
Fire 1
Fire 2
Fire 3
Fire 4
Fire frequency gradient

Fig. 6

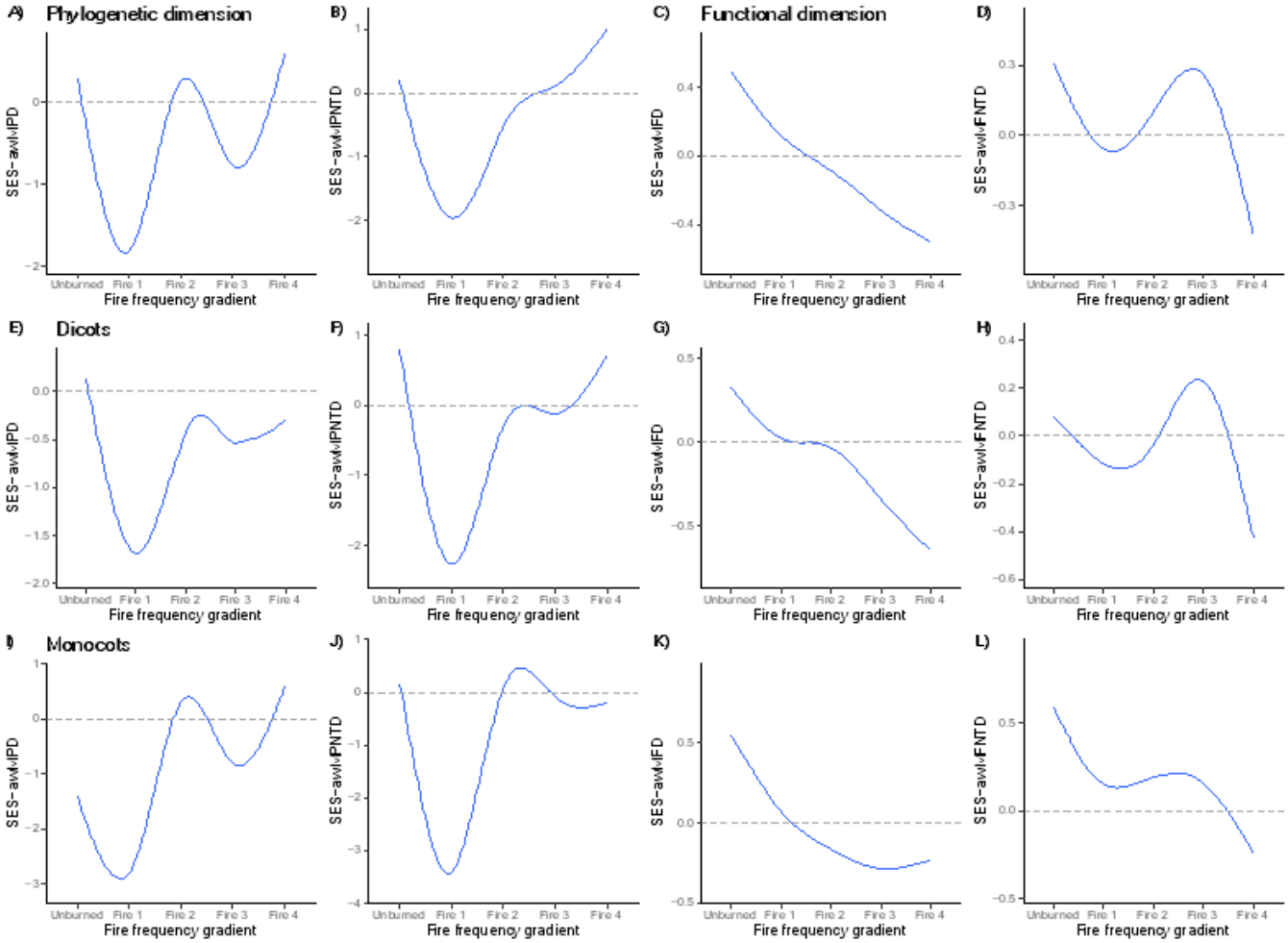
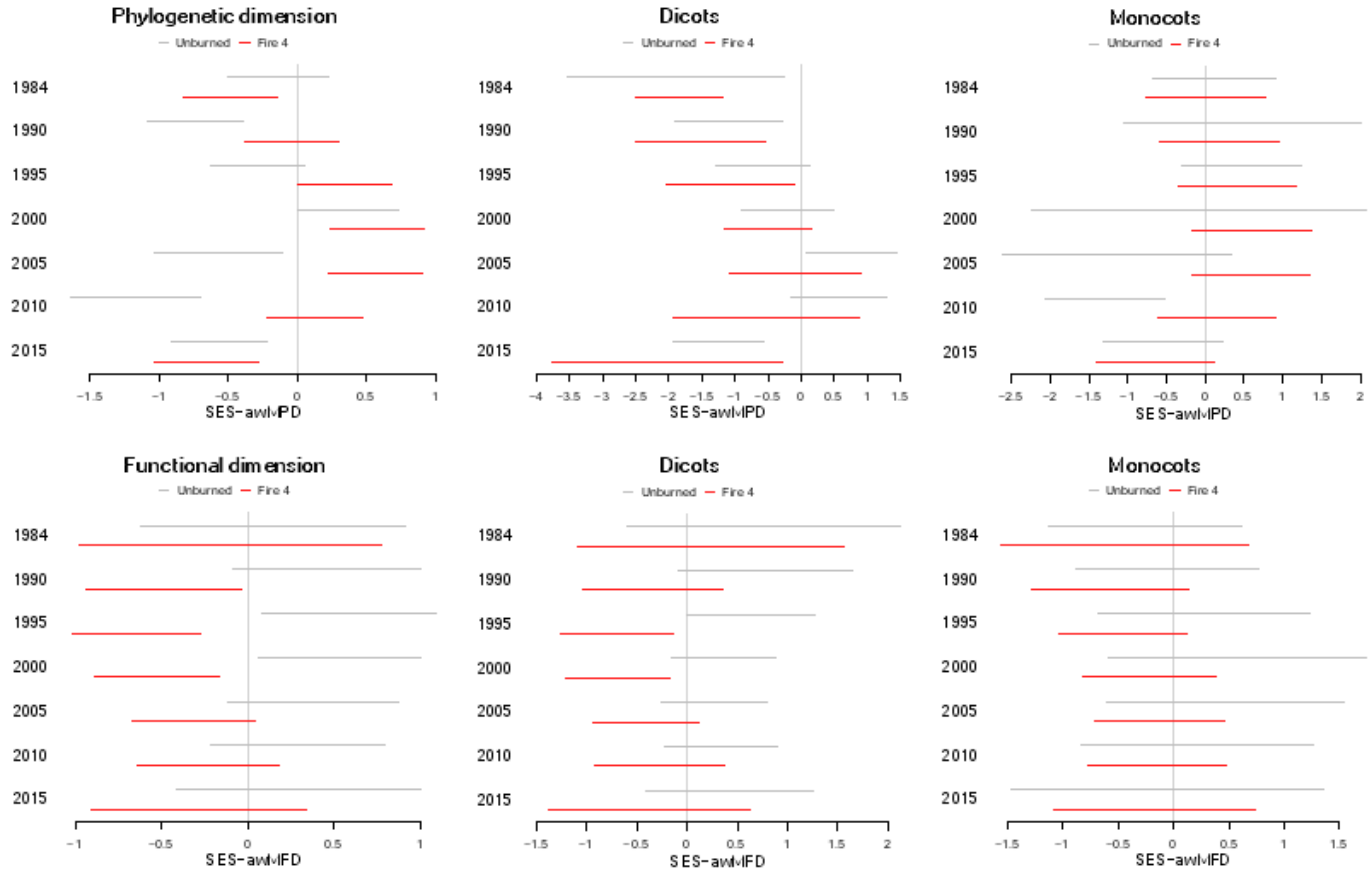

A) Phylogenetic dimension
B)
C) Functional dimension
D)
E) Dicots
F)
G)
H)
I) Monocots
J)
K)
L)
SES-awlvPD
SES-awlvPNTD
SES-awlvFD
SES-awlvFNTD
Unburned Fire 1 Fire 2 Fire 3 Fire 4
Fire frequency gradient

Fig. 7

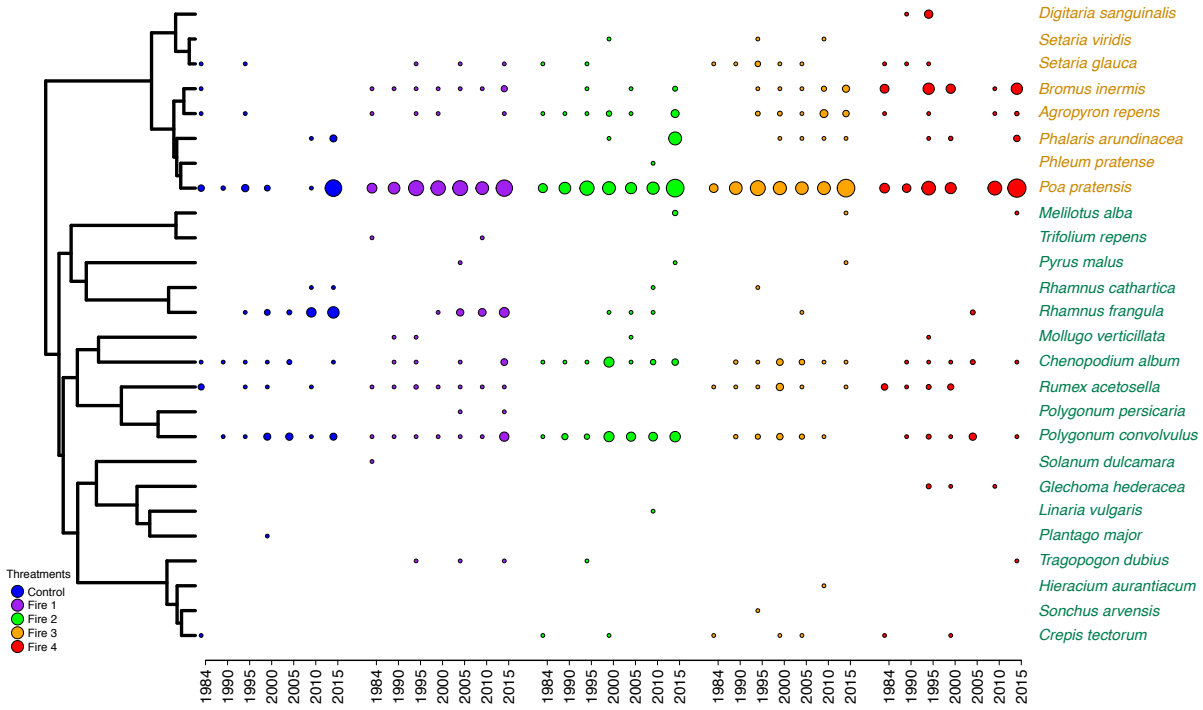

Phylogenetic dimension
Dicots
Monocots
Unburned Fire 4
1984
1990
1995
2000
2005
2010
2015
SES-awlvPD
Functional dimension
SES-awlvFD

ECOLOGICAL MONOGRAPHS

TESTING DARWIN'S NATURALIZATION CONUNDRUM BASED ON TAXONOMIC, PHYLOGENETIC AND FUNCTIONAL DIMENSIONS OF VASCULAR PLANTS

Jesús N. Pinto-Ledezma, Fabricio Villalobos, Peter B. Reich, Jane A. Catford, Daniel J. Larkin, Jeannine Cavender-Bares

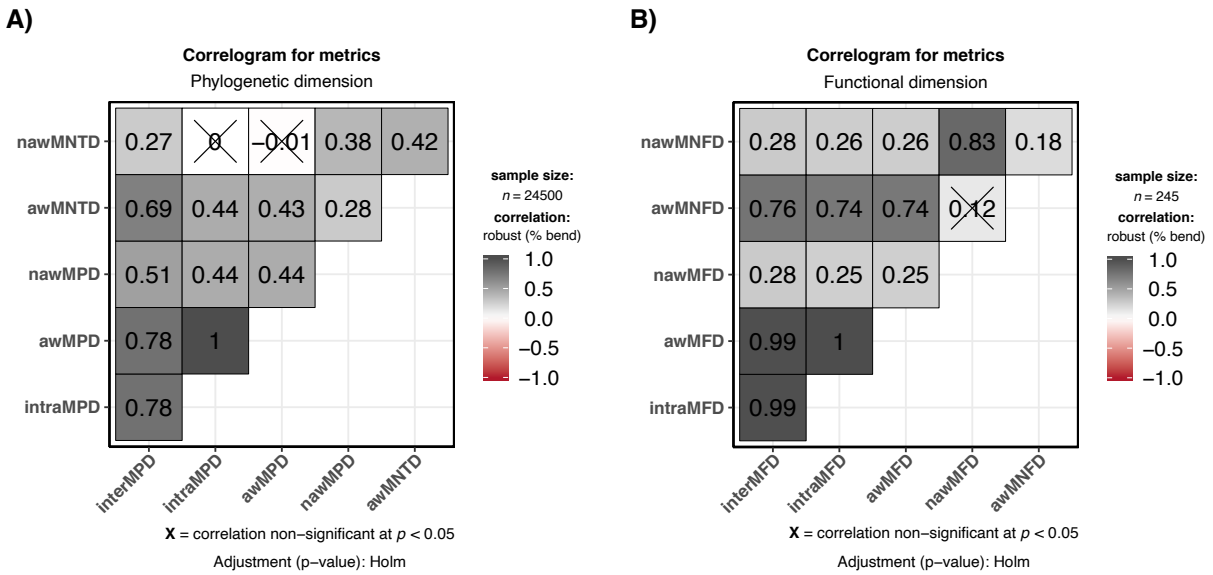
Appendix Fig. S1. Relative abundance of nonnative species in the oak savanna understory permanent plots at Cedar Creek Ecosystem Science Reserve, Minnesota, USA. Colors depict the fire treatment and circle sizes are proportional to the relative abundance (log transformed) averaged by fire treatment. Species names are colored according the major groups of vascular plants; monocots = orange and dicots = green.



14

15 **Appendix Fig. S2.** Correlation matrices for the metrics of phylogenetic and functional

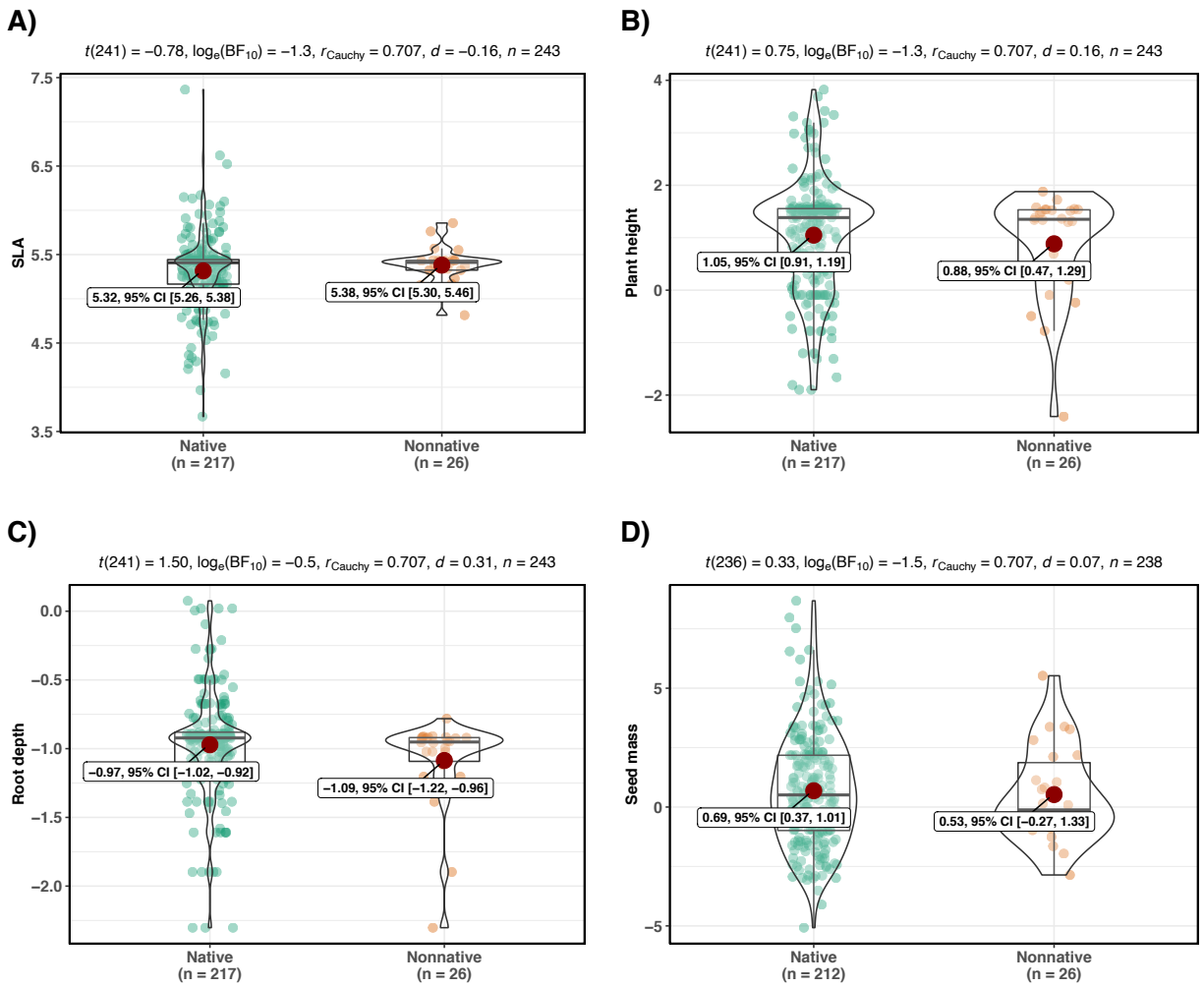
16 dimensions evaluated in this study.



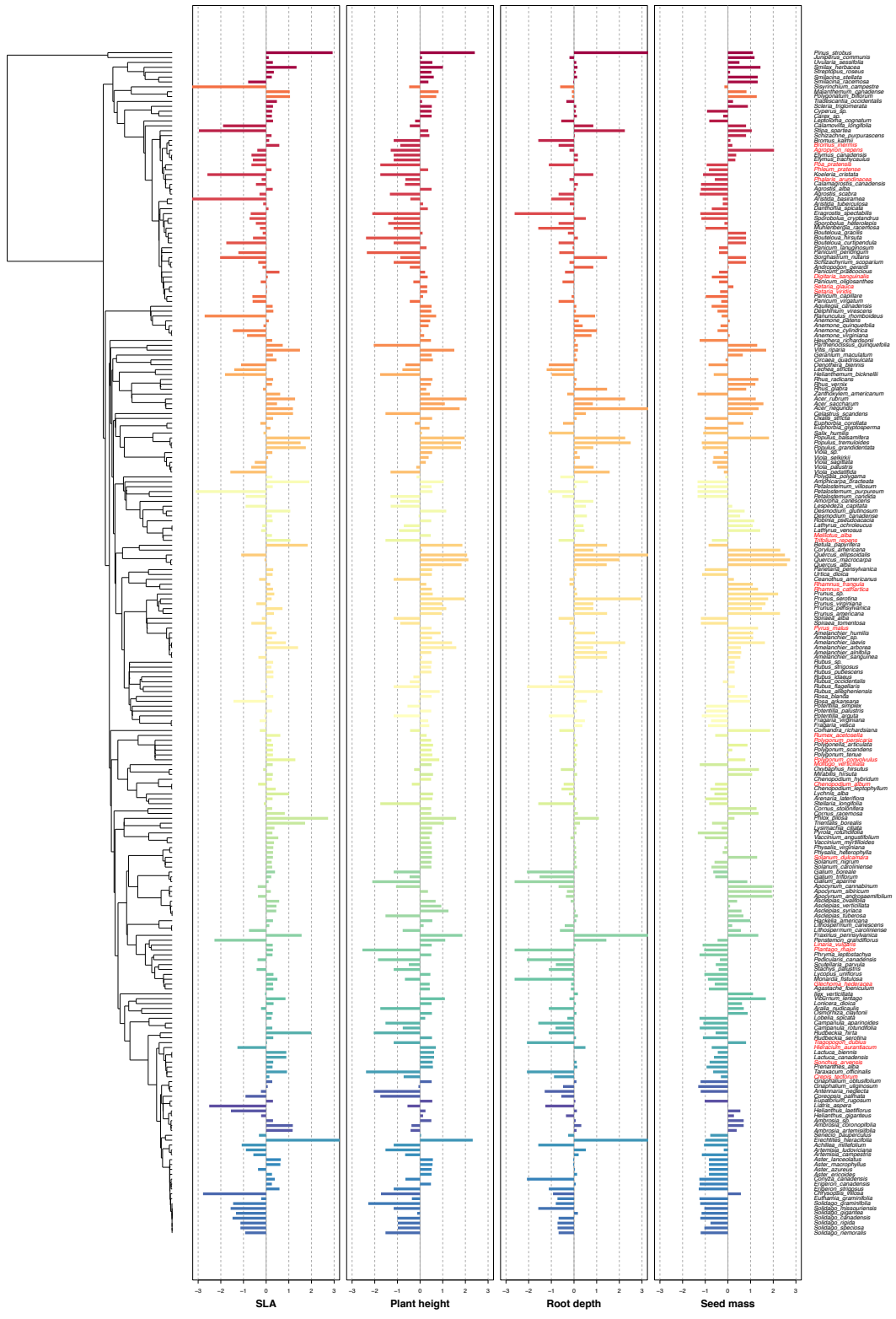
17

18

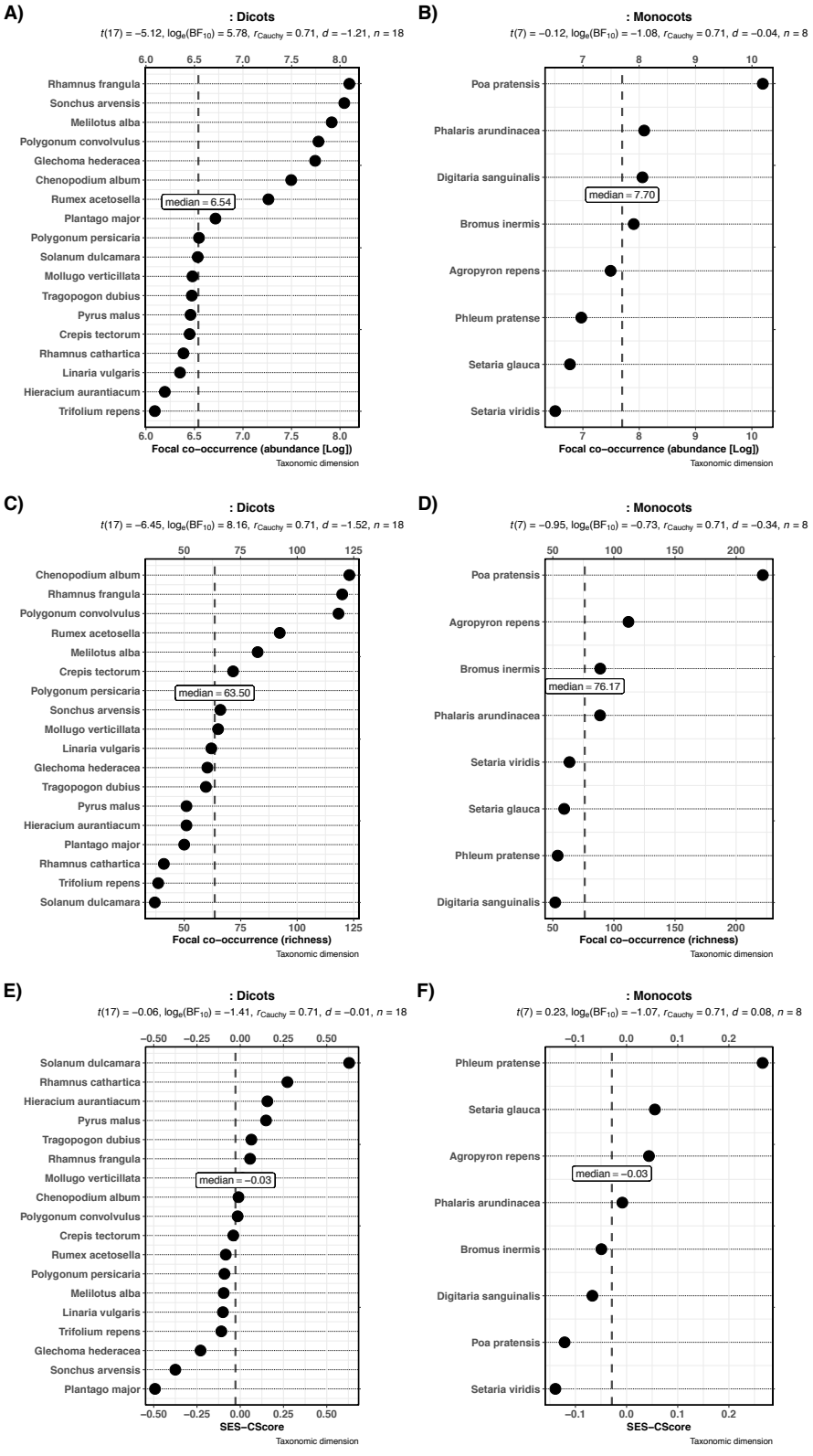
Appendix Fig. S3. Comparison of functional traits between native and nonnative species. A) SLA, B) plant height, C) rooting depth, and d) seed mass.



Appendix Fig. S4. Maximum clade credibility tree obtained from 1000 trees and the distribution of the four functional traits (log transformed for graphical representation) used in this study in which each color bar correspond to a specific species. Species names in red correspond to nonnative species.

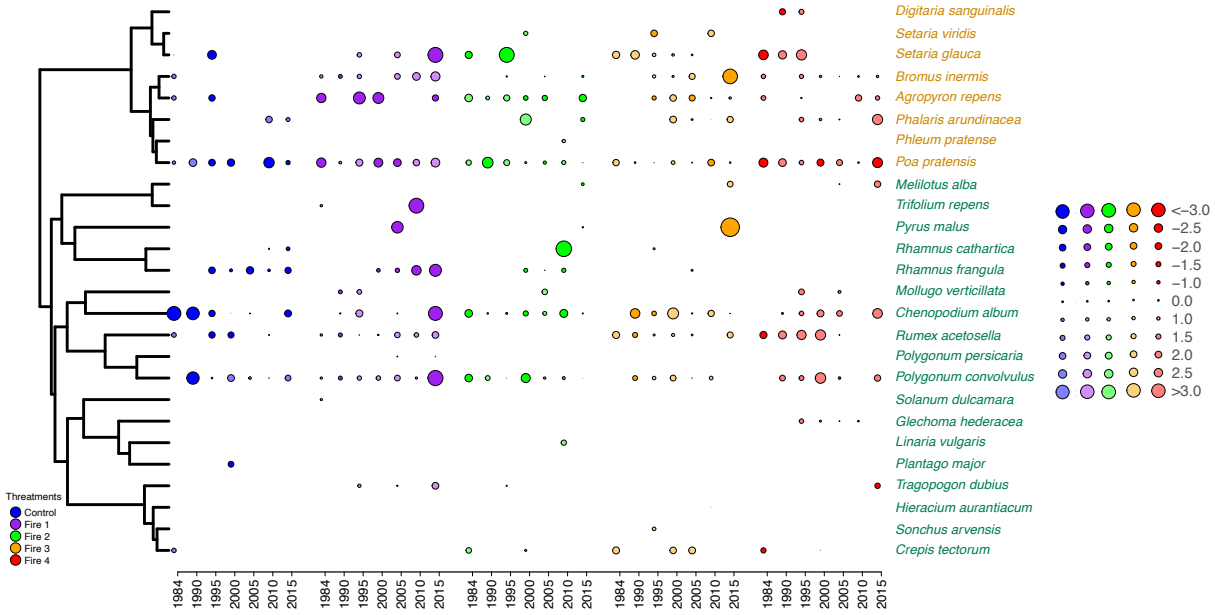

SLA
Plant height
Root depth
Seed mass

Appendix Fig. S5. Patterns of co-occurrence for the taxonomic dimension over time and across the fire frequency gradient. Values correspond to the three metrics used to estimate the co-occurrence patterns for the taxonomic dimension averaged across all permanent plots (landscape scale). A-B) Co-occurrence estimated by recording the abundance and identity of species co-occurring with a focal-nonnative species. C-D) Co-occurrence estimated by recording the presence-absence and identity of species co-occurring with a focal-nonnative species. E-F) Co-occurrence estimated using the C-Score metric.


A)
: Dicots
t(17) = −5.12, log_e(BF_10) = 5.78, r_Cauchy = 0.71, d = −1.21, n = 18
Rhamnus frangula
Sonchus arvensis
Melilotus alba
Polygonum convolvulus
Glechoma hederacea
Chenopodium album
Rumex acetosella
median = 6.54
Plantago major
Polygonum persicaria
Solanum dulcamara
Mollugo verticillata
Tragopogon dubius
Pyrus malus
Crepis tectorum
Rhamnus cathartica
Linaria vulgaris
Hieracium aurantiacum
Trifolium repens
6.0 6.5 7.0 7.5 8.0
Focal co−occurrence (abundance [Log])
Taxonomic dimension
B)
: Monocots
t(7) = −0.12, log_e(BF_10) = −1.08, r_Cauchy = 0.71, d = −0.04, n = 8
Poa pratensis
Phalaris arundinacea
Digitaria sanguinalis
median = 7.70
Bromus inermis
Agropyron repens
Phleum pratense
Setaria glauca
Setaria viridis
7 8 9 10
Focal co−occurrence (abundance [Log])
Taxonomic dimension
C)
: Dicots
t(17) = −6.45, log_e(BF_10) = 8.16, r_Cauchy = 0.71, d = −1.52, n = 18
Chenopodium album
Rhamnus frangula
Polygonum convolvulus
Rumex acetosella
Melilotus alba
Crepis tectorum
Polygonum persicaria
median = 63.50
Sonchus arvensis
Mollugo verticillata
Linaria vulgaris
Glechoma hederacea
Tragopogon dubius
Pyrus malus
Hieracium aurantiacum
Plantago major
Rhamnus cathartica
Trifolium repens
Solanum dulcamara
50 75 100 125
Focal co−occurrence (richness)
Taxonomic dimension
D)
: Monocots
t(7) = −0.95, log_e(BF_10) = −0.73, r_Cauchy = 0.71, d = −0.34, n = 8
Poa pratensis
Agropyron repens
Bromus inermis
median = 76.17
Phalaris arundinacea
Setaria viridis
Setaria glauca
Phleum pratense
Digitaria sanguinalis
50 100 150 200
Focal co−occurrence (richness)
Taxonomic dimension
E)
: Dicots
t(17) = −0.06, log_e(BF_10) = −1.41, r_Cauchy = 0.71, d = −0.01, n = 18
Solanum dulcamara
Rhamnus cathartica
Hieracium aurantiacum
Pyrus malus
Tragopogon dubius
Rhamnus frangula
Mollugo verticillata
median = −0.03
Chenopodium album
Polygonum convolvulus
Crepis tectorum
Rumex acetosella
Polygonum persicaria
Melilotus alba
Linaria vulgaris
Trifolium repens
Glechoma hederacea
Sonchus arvensis
Plantago major
−0.50 −0.25 0.00 0.25 0.50
SES−CScore
Taxonomic dimension
F)
: Monocots
t(7) = 0.23, log_e(BF_10) = −1.07, r_Cauchy = 0.71, d = 0.08, n = 8
Phleum pratense
Setaria glauca
Agropyron repens
median = −0.03
Phalaris arundinacea
Bromus inermis
Digitaria sanguinalis
Poa pratensis
Setaria viridis
−0.1 0.0 0.1 0.2
SES−CScore
Taxonomic dimension

Appendix Fig. S6. Patterns of phylogenetic structure of focal nonnative species over time and across the experimental fire gradient. Darker and lighter colors correspond to phylogenetic clustering and phylogenetic overdispersion, respectively.

Appendix Fig. S7. Patterns of functional structure of focal nonnative species over time and across the experimental fire gradient. Darker and lighter colors correspond to functional clustering and functional overdispersion, respectively.



48

49 **Appendix Table S1.** Species for which trait values were averaged from genus-level.

Species	Value	Trait
Euthamia graminifolia	21.7326188	SLA
Hackelia americana	23.95256848	SLA
Heuchera richardsonii	22.150322	SLA
Mirabilis hirsuta	19.89202581	SLA
Muhlenbergia racemosa	26.46470061	SLA
Petalostemum villosum	23.45284671	SLA
Phryma leptostachya	72.59617729	SLA
Polygonella articulata	27.92740083	SLA
Schizachne purpurascens	26.46470061	SLA
Scleria triglomerata	21.42986974	SLA
Uvularia sessifolia	21.632	SLA
Amphicarpa bracteata	10.4322658	Plant heigth
Bouteloua gracilis	0.32218989	Plant heigth
Chrysopsis villosa	0.43282982	Plant heigth
Euthamia graminifolia	0.43282982	Plant heigth
Hackelia americana	4.88164787	Plant heigth
Mirabilis hirsuta	5.23545058	Plant heigth
Oxybaphus hirsutus	5.23545058	Plant heigth
Petalostemum candida	10.4322658	Plant heigth
Petalostemum purpureum	10.4322658	Plant heigth
Petalostemum villosum	10.4322658	Plant heigth
Phryma leptostachya	0.48053571	Plant heigth
Schizachne purpurascens	0.32218989	Plant heigth
Uvularia sessifolia	0.225	Plant heigth
Apocynum androsaemifolium	196.3122254	Seed mass
Apocynum cannabinum	196.3122254	Seed mass
Apocynum sibiricum	214.4047415	Seed mass
Eurybia macrophylla	5.645410273	Seed mass
Bouteloua curtipendula	8.839506508	Seed mass
Chondrosum gracile	8.839506508	Seed mass
Chondrosum hirsutum	8.839506508	Seed mass
Calamovilfa longifolia	8.839506508	Seed mass
Comandra umbellata	137.2047586	Seed mass
Lechea stricta	2.074883797	Seed mass

Phryma leptostachya	0.051123276	Seed mass
Polygonella articulata	111.537202	Seed mass
Nabalus albus	5.645410273	Seed mass
Schizachne purpurascens	8.839506508	Seed mass
Scleria triglomerata	10.43507808	Seed mass
Sorghastrum nutans	8.839506508	Seed mass
Aristida basiramea	0.025001809	Rooting depth
Danthonia spicata	0.005378182	Rooting depth
Digitaria sanguinalis	0.119356885	Rooting depth
Panicum capillare	0.3	Rooting depth
Phleum pratense	0.4774286	Rooting depth
Setaria viridis	0.104277241	Rooting depth
Stipa spartea	0.02859375	Rooting depth